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## COMPARISON OF CONFORMATION, ANATOMY, AND SKELETAL STRUCTURE OF A HIGHLY SPECIALIZED DAIRY COW AND A HIGHLY SPECIALIZED BEEF COW [1]


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### INTRODUCTION

Dairy type and beef type in cattle are fairly definite. The two types show great contrast outwardly. Much has been written concerning the relative quantity and quality of the edible portions of the carcasses of animals representing the two types, but the differences between their skeletal and anatomical structures have not been clearly brought out.

Because of the emphasis given to the angular, triple wedge shape of the dairy animal and to the blocky form of the beef animal, the tendency has been to imply that the difference between the two types is greater than can be accounted for by the difference in fleshing and that it must extend to the anatomical and skeletal structure of the animal.

A project having for its object the determination of the relationship of the conformation and anatomy of a dairy cow to her milk and butterfat producing capacity has been in progress for some time. Comparative measurements of the external conformation and the size of the internal organs have already been made on a large number of cows. Sophie 19th of Hood Farm, a noted purebred Jersey cow, was presented to the Bureau of Dairy Industry in order that her conformation and anatomy might be studied. This cow, with a production of 17,557.8 pounds of milk and 999.1 pounds of butterfat in one year, held the world's record for the Jersey breed from January 20, 1914, to November 30, 1918. She also had the distinction of having produced 7,544.51 pounds of butterfat in 11 official yearly records. This is the world's record for lifetime butterfat production for Jersey cows. Although this cow did not possess the beauty of type which would have enabled her to win in show-ring competition, her achievements as a producer and as a breeder are sufficient to classify her as an outstanding dairy cow and a representative of the dairy type in its truest sense. Not only was a study made of her conformation and anatomy, but of her skeleton as well.

A need was felt for a comparative study of the conformation, anatomy, and skeletal structure of a cow representing the extreme beef type. For this purpose the purebred Aberdeen Angus cow, Blackbird of Dallas, was obtained. She was selected as a typical representative of this type because she had been a grand champion at the Illinois State Fair and a consistent winner in the show ring


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for a number of years. She also was a persistent breeder, having produced eight calves. Nothing, however, is known of her ability to produce milk or butterfat, except that she was said to have been a good milker for a beef cow.

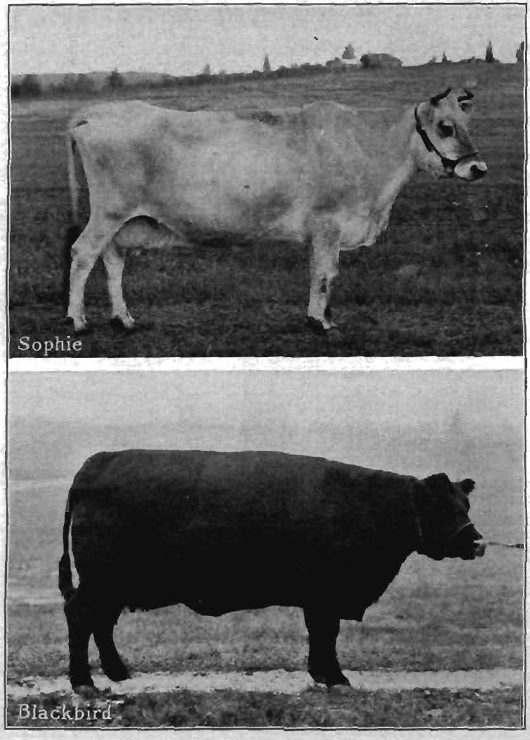


FIG. 1.—Side views of Sophie and Blackbird

For purposes of brevity, these cows will subsequently be referred to as Sophie and Blackbird.

Sophie probably would have been considered a relatively large individual in a breed that, on the basis of weight, is the smallest of

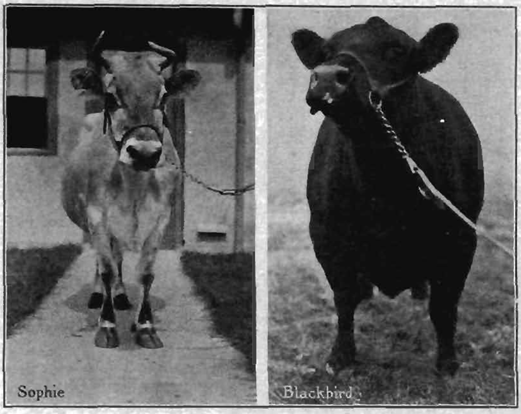


FIG. 2.—Front views of Sophie and Blackbird

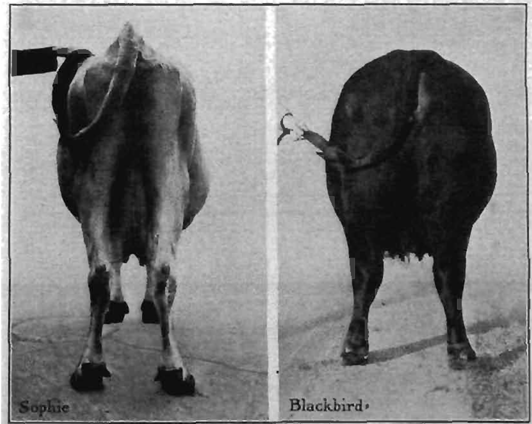


FIG. 3.—Rear views of Sophie and Blackbird

relatively large individual in a beef breed that, in weight, ranks below both the Shorthorn and the Hereford. When obtained, both these cows were well advanced in age. They had ceased to be breeders and had been nonlactating for an extended period. Sophie was dry for 3 or 4 months after a lactation period of 18 months. Blackbird was dry 25 months after a lactation period of 7 months. For comparative purposes these two cows are considered satisfactory to represent the highly specialized dairy type and the highly specialized beef type of cattle. Comparative photographs are shown in Figures 1, 2, and 3.

## ANTE-MORTEM DATA

In order to make possible an analysis of the external differences between the two cows, the type of each was translated into numerical values through the application of external body measurements. The plan of measuring was the same as that used by the Bureau of Dairy Industry in studying body development and in determining the relationship of the conformation and anatomy of a dairy cow to her milk and butterfat producing capacity.

Blackbird was in a condition of very high flesh, having been exhibited at the International Livestock Exposition a short time before the measurements were obtained. Difficulty was experienced, therefore, in locating some of the points of anatomy at which measurements were taken. The external measurements representing type or conformation are given in Table 1.

TABLE 1.—*Ante-mortem external measurements of Sophie and Blackbird*

| Item | Sophie | Blackbird | Relation of Blackbird's measurements to those of Sophie |
|---|---|---|---|
| | | | *Per cent* |
| Age ... years | 10 | 12 | |
| Thickness of hide ... cm | 0.66 | 1.32 | 200.0 |
| Live weight ... pounds | 927.00 | 1,565.00 | 168.8 |
| Height at withers ... cm | 128.17 | 122.13 | 95.3 |
| Height at hips ... cm | 122.50 | 121.71 | 99.4 |
| Height at pin bones ... cm | 117.00 | 119.25 | 101.9 |
| Length, top hips to top pin bones ... cm | 41.00 | 41.50 | 101.2 |
| Depth of fore chest ... cm | 71.50 | 75.00 | 104.9 |
| Depth of rear chest ... cm | 71.00 | 78.25 | 110.2 |
| Depth of paunch ... cm | 71.17 | 80.25 | 112.8 |
| Width of fore chest ... cm | 36.17 | 61.00 | 168.7 |
| Width of rear chest ... cm | 56.33 | 65.75 | 116.0 |
| Width of paunch ... cm | 60.17 | 73.75 | 122.6 |
| Width of hips ... cm | 48.00 | 65.50 | 136.5 |
| Width of pin bones ... cm | 29.50 | 34.50 | 116.9 |
| Width of thurls ... cm | 43.00 | 52.38 | 121.8 |
| Width of loin ... cm | 29.00 | ... | ... |
| Length from withers to hips ... cm | 88.50 | 86.50 | 97.7 |
| Length from hips to pin bones (tape line) ... cm | 53.00 | 49.00 | 92.5 |
| Total length from withers to pin bones ... cm | 141.50 | 135.50 | 95.8 |
| Length of loin ... cm | 38.00 | ... | ... |
| Circumference of fore chest ... cm | 177.67 | 230.00 | 129.5 |
| Circumference of rear chest ... cm | 203.67 | 241.50 | 118.6 |
| Circumference of paunch ... cm | 213.67 | 261.00 | 122.2 |
| Width of forehead (tape line) ... cm | 22.00 | 24.25 | 110.2 |
| Circumference of muzzle ... cm | 44.00 | 47.75 | 108.5 |
| Length from poll to mouth (tape line) ... cm | 56.00 | 54.50 | 97.3 |
| Circumference of shin bone ... cm | 16.50 | 18.75 | 113.6 |

As a supplement to the measurements recorded in Table 1, cross-section outlines or contours were made, and a number of values were calculated from the data taken. A discussion of the derivation of these supplementary data will be followed by a general comparative discussion of all the ante-mortem data and of the determinations made on these two cows.

Cross-section outlines or contours of the fore chest and paunch (figs. 4 and 5) were made for both Sophie and Blackbird. They were made by original methods and with specially constructed equipment, and were drawn life-size on specially ruled sheets of paper. The inner curve in each figure is the cross-section outline of the fore chest; the outer curve is the corresponding outline of the paunch. A striking difference in conformation between the two cows is shown by these contours. Coutours are much more siguificant than caliper measurements of the same body parts because it is possible that two cows may have exactly the same vertical and transverse diameters, yet, because of differences in outline, they may differ widely in cross-section areas. The areas of these contours were measured with a planimeter and are given in Table 2.

TABLE 2.—*Contour areas of fore chest and paunch of Sophie and Blackbird*

| Cow | Fore chest | Paunch |
|---|---|---|
| | *Sq. cm.* | *Sq. cm.* |
| Sophie | 1,882 | 3,226 |
| Blackbird | 3,960 | 4,916 |

The contour area of the fore chest of Blackbird was 210.4 per cent of that of Sophie, and the contour area of her paunch was 152.4 per cent of that of Sophie. The area of Sophie's fore chest was only 58.3 per cent of the area of her paunch, whereas Blackbird's fore chest area was 80.6 per cent of the area of her paunch.

The following values, which were calculated from the ante-mortem data, are presented to show more completely the relative conformation of the two cows:

(1) The angle of inclination or slope of rump was calculated on the basis of the height at hip, height at pin bone, and the linear distance between them. This angle was 7° 43′ for Sophie and 3° 24′ for Blackbird. The angle was only 44.1 per cent as great for Blackbird as for Sophie.

(2) The thoracic index, which is the relation of depth to width of fore chest, was determined by dividing the former by the latter, giving indexes of 1.977 for Sophie and 1.230 for Blackbird.

(3) The abdominal index, which shows the relation of depth to width of paunch, was determined in a similar manner. Abdominal indexes were 1.183 for Sophie and 1.088 for Blackbird.

(4) A value designed to represent the approximate volume of barrel was determined more or less arbitrarily by multiplying the average of the fore chest and paunch contour areas by the length from withers to line between hips. These two volumes, as determined, were 226,029 c. c. for Sophie and 383,887 c. c. for Blackbird. Blackbird had a volume 169.8 per cent of that of Sophie.

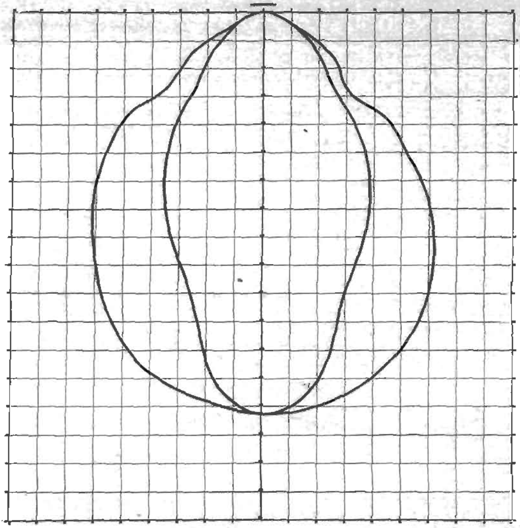

FIG. 4.—Contours of Sophie's fore chest and paunch

(5) The body-surface area was calculated according to the following formula of Hogan and Skouby[2]: $S=W^{.4}\times L^{.6}\times K$, in which $S$= surface area of body in square centimeters, $W$=live weight in kilograms, $L$=length from withers to pin bones in centimeters, and K=217, a constant value for cattle. Since in this comparison the formula was applied to animals of extremely different type and degree of fleshing, there may be some question as to the accuracy of the areas determined, which were 47,460 sq. cm. for Sophie and 57,000 sq. cm. for Blackbird. On this basis the surface area of Blackbird was 120.1 per cent of that of Sophie.

(6) The legginess, or proportion of length of legs to total height, was calculated by subtracting depth of fore chest from height at withers and dividing the difference by the height at withers. Values determined for Sophie and Blackbird were 0.442 and 0.386 respectively.

(7) The relative wedge shape, or difference between paunch and fore chest in depth, width, and circumference, was determined (*a*) in actual units of measurement and (*b*) in the form of a ratio of paunch to fore-chest dimensions. The differences in measurements and the calculated ratios are shown in Table 3.

[2] HOGAN, A. G., and SKOUBY, C. I. DETERMINATION OF THE SURFACE AREA OF CATTLE AND SWINE. Jour. Agr. Research 25: 419–430. 1923.

TABLE 3.—*Relative wedge shape of Sophie and Blackbird as shown by differences in and ratios of fore-chest and paunch measurements*

| Item | Sophie | Blackbird |
|---|---|---|
| Differences in measurements: | | |
| Depth of paunch minus depth of fore chest ..........cm.. | −0.33 | +5.25 |
| Width of paunch minus width of fore chest ..........cm.. | +24.00 | +12.75 |
| Circumference of paunch minus circumference of fore chest ..........cm.. | +36.00 | +31.00 |
| Ratios of measurements: | | |
| Depth of paunch to depth of fore chest | .995 | 1.070 |
| Width of paunch to width of fore chest | 1.664 | 1.209 |
| Circumference of paunch to circumference of fore chest | 1.203 | 1.135 |

Although Sophie weighed 638 pounds less than Blackbird when ante-mortem data were obtained, she was more than 6 cm. taller at the withers. Blackbird was considerably deeper in body throughout and actually had a far greater vertical wedge shape, as indicated by the increase in depth of rear chest and of paunch over fore chest. Sophie had almost parallel back and belly lines, whereas those of Blackbird were divergent to the extent of more than 5 cm. In width of body, however, Sophie had almost twice as much wedge shape as did Blackbird, but was much narrower throughout. In fact, the ante-mortem measurements, the contours, and the calculated ratios and factors consistently show that Sophie was decidedly

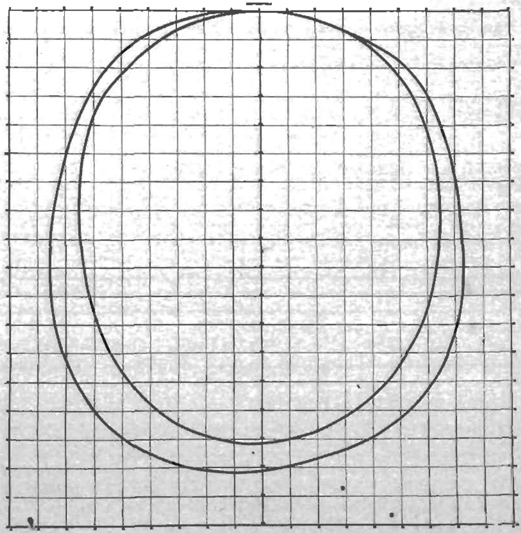

FIG. 5.—Contours of Blackbird's fore chest and paunch

tapering laterally from front to rear but had almost equal depth of fore chest and of paunch. Blackbird, on the contrary, did not taper greatly laterally from front to rear but did show a decided increase in depth of paunch over depth of fore chest.

Measurements from withers to a line between hips and from a line between hips to pin bones taken with a tape line were greater in each case for Sophie than for Blackbird. Sophie, therefore, was not only taller than Blackbird but was also longer in body. The differences in height, however, are relatively slight. Blackbird was 95.3 per cent as tall as Sophie at the withers, 99.4 per cent at the hips, and 101.9 per cent at the pin bones. The average of these three comparative heights shows that Blackbird was 98.8 per cent as tall as Sophie. The total length of Blackbird from withers to pin bones was 95.8 per cent as great as that of Sophie. The external height and length of body of the two cows, therefore, was not strikingly different but was slightly less for Blackbird than for Sophie. The three circumferences of body indicated considerably greater size for Blackbird but a slightly greater wedge shape for Sophie. Blackbird had a greater width of forehead and circumference of muzzle, whereas Sophie had a slightly greater length of head. The shin bone, or metacarpus, appeared to be heavier in the beef cow.

Sophie carried very little body fat. Blackbird, on the contrary, was excessively fat. After she was killed, the layer of subcutaneous fat at the spine in the region of the loin, as nearly as it could be measured, was from 6 to 7 cm. in thickness. The layer of subcutaneous fat at the tenth rib appeared to be from 8 to 9 cm. in thickness. It is obvious that the fleshing may have influenced the different measurements of the beef cow in varying degrees. Although this condition made difficult the location of the hip points and pin bones of Blackbird, it appeared that she was considerably more nearly level in the rump than was Sophie. The fact that the thoracic index of Sophie was much greater than that of Blackbird indicated that in the fore chest she was relatively much deeper in proportion to width than was Blackbird. The abdominal index of the two cows was only slightly different but showed that in the paunch also Sophie was slightly deeper in proportion to her width than was Blackbird. The volume of barrel appeared to be distinctly greater for Blackbird than for Sophie. The body-surface area of Blackbird also appeared to be greater than that of Sophie to the extent of about 20 per cent. The legginess of Sophie appeared to be approximately 15 per cent greater than that of Blackbird.

In Table 1 the only measurements which are lower for Blackbird than for Sophie are the height at withers, height at hips, length from withers to hips, length from hips to pin bones, total length from withers to pin bones, and length from poll to mouth. These signify height of body, length of body, and length of head, all of which may be considered as "scale." Of those values which are greater for Blackbird than for Sophie only five show a difference in excess of 25 per cent. These are thickness of hide, live weight, width of fore chest, width of hips, and circumference of fore chest. It appears that each of these five differences may be largely attributed to Blackbird's heavy fleshing and excessive fat deposition.

## POST-MORTEM DATA

In accordance with the plan that has been adopted by this bureau in studying the relationship of conformation and anatomy to producing capacity, the two cows were slaughtered and post-mortem data of both were obtained. Since the skeletons were to be preserved it was necessary that the animals be killed without injury to any bony part.

Sophie was killed by injection of chloroform into the blood stream. Blackbird was killed by bleeding. Sophie's lungs and liver retained large quantities of coagulated blood, and consequently the weight of those organs was excessive. Blackbird's organs when weighed were all practically free of blood. Comparative weight of organs of the two cows, therefore, is not entirely complete. Furthermore, since the skeleton could not be cut or injured, it was impossible to obtain for weighing such organs as the brain and pituitary body. The organs which are available and not affected by retention of blood are listed for comparison in Table 4.

TABLE 4.—*Post-mortem data of Sophie and Blackbird*

| Item | Sophie | | Blackbird | | Relation of Blackbird's data to those of Sophie | |
|---|---|---|---|---|---|---|
| | Weight or measurement of part | Units of weight or measurement per 100 pounds empty body weight | Weight or measurement of part | Units of weight or measurement per 100 pounds empty body weight | Actual units | Units per 100 pounds empty body weight |
| | | | | | *Per cent* | *Per cent* |
| Empty body weight ... pounds | 768.5 | ------ | 1,476.3 | ------ | 192.1 | ------ |
| Weight of hide ... do | 55.00 | 7.16 | 82.50 | 5.59 | 150.0 | 78.1 |
| Weight of ovaries ... grams | 25.00 | 3.25 | 34.40 | 2.33 | 137.6 | 71.7 |
| Weight of pancreas ... do | (a) | ------ | 371.00 | 25.13 | ------ | ------ |
| Weight of kidneys ... pounds | 3.19 | .42 | 3.85 | .26 | 120.7 | 61.9 |
| Weight of adrenals ... grams | 37.00 | 4.81 | 57.50 | 3.89 | 155.4 | 80.9 |
| Weight of spleen ... pounds | 1.81 | .24 | 1.85 | .13 | 102.2 | 54.2 |
| Weight of liver ... do | (b) | ------ | 14.75 | 1.00 | ------ | ------ |
| Weight of small intestine ... do | 13.00 | 1.69 | 8.70 | .59 | 66.9 | 34.9 |
| Weight of large intestine ... do | 22.50 | 2.93 | 7.75 | .52 | 34.4 | 17.7 |
| Total weight of intestines ... do | 35.50 | 4.62 | 16.45 | 1.11 | 46.3 | 24.0 |
| Weight of intestinal contents ... do | 32.00 | ------ | 19.05 | ------ | 59.5 | ------ |
| Length of small intestine ... feet | 132.50 | 17.24 | 140.22 | 9.50 | 105.8 | 55.1 |
| Length of large intestine ... do | 34.00 | 4.42 | 41.49 | 2.81 | 122.0 | 63.6 |
| Total length of intestines ... do | 166.50 | 21.67 | 181.71 | 12.31 | 109.1 | 56.8 |
| Total weight of empty stomachs ... pounds | 47.00 | 6.12 | 31.35 | 2.12 | 66.7 | 34.6 |
| Weight of stomach contents ... do | 126.50 | ------ | 89.65 | ------ | 70.9 | ------ |
| Total weight of abdominal fat ... do | 34.63 | 4.51 | 87.15 | 5.90 | 251.7 | 130.8 |
| Weight of right lung ... do | (c) | ------ | 3.15 | .21 | ------ | ------ |
| Weight of left lung ... do | ------ | ------ | 2.70 | .18 | ------ | ------ |
| Total weight of lungs ... do | ------ | ------ | 5.85 | .40 | ------ | ------ |
| Circumference of heart (near base) ... centimeters | 45.00 | 5.86 | 43.50 | 2.95 | 96.7 | 50.3 |
| Circumference of heart (over apex) ... do | 48.00 | 6.25 | 51.75 | 3.51 | 107.8 | 56.2 |
| Weight of heart (trimmed close) ... pounds | 3.94 | .51 | 3.90 | .26 | 99.0 | 51.0 |
| Weight of thoracic fat ... do | 5.50 | .72 | 8.75 | .59 | 159.1 | 81.9 |
| Weight of thyroid ... grams | 23.00 | 2.99 | 57.50 | 3.89 | 250.0 | 130.1 |

[a] Pancreas omitted. [b] Liver abnormal. [c] Lungs filled with clotted blood.

Empty body weight is more dependable than live weight, because it eliminates variations due to " fill " of feed or water before weighing or those due to differences in the intervals between feeding or watering and time of weighing. It is determined by subtracting the total weight of contents of stomachs and intestines from the live weight.

The live weights of Sophie and of Blackbird immediately before slaughter were 927 pounds and 1,585 pounds, respectively. Although this difference in live weight between the two cows was only 658 pounds, the difference in empty body weight at time of slaughter was 707.8 pounds.

The number of units of weight or measurement of each organ or part for every 100 pounds of empty body weight has been calculated for both cows to show the relation which each organ or part bears to the total animal structure. These values, in addition to the weight or measurement of the individual organs or parts, are given in Table 4. As one might anticipate, the values for each 100 pounds of empty body weight were found to be relatively much lower for Blackbird than for Sophie. The last two columns in Table 4 show in terms of percentage the relation of the size of organs or parts of Blackbird to those of Sophie, on the basis of (1) the actual units of measure, and (2) the units per 100 pounds of empty body weight.

The determination of the weight of empty intestines is at best subject to some difficulty because of inability to remove all the fat. The length of intestines, on the contrary, is readily determined. The lengths of 166.5 feet for Sophie and 181.71 feet for Blackbird are of interest because of their relative similarity and because these values are intermediate and do not even approach the maximum or the minimum intestine lengths recorded in the post-mortem studies previously referred to.

The lung weights of Sophie were unavailable on account of blood retention. The total lung weight of Blackbird was 5.85 pounds. This is relatively low on the basis of the average of 229 cows slaughtered in a packing house. Although the average empty body weight of these 229 cows was only 941 pounds, the average total lung weight was 7.36 pounds. The weight of Blackbird's lungs was only 0.4 pound per 100 pounds empty body weight, whereas the 229 cows averaged 0.78 pound per 100 pounds empty body weight.

The hearts of Sophie and Blackbird were similar in measurements and almost identical in weight. Each of these hearts, however, was about one-half pound in actual weight below the average weights of 247 hearts obtained in the packing house. Sophie had 0.51 pound, Blackbird 0.26 pound, and the 247 packing-house cows averaged 0.47 pound of heart weight for each 100 pounds empty body weight. The heart weight of Blackbird appears, therefore, to be low in number of pounds and in relation to her empty body weight when compared with data obtained from the 247 cows slaughtered in a packing house.

The only instances in which the actual units of weight or measurement listed in Table 4 are even slightly lower for Blackbird than for Sophie are weight of empty intestines, weight of intestine contents, weight of empty stomachs, weight of stomach contents, and weight and one circumference of heart. As already pointed out, the heart weights and measurements, although differing very slightly, are approximately the same for both cows.

However, since the empty body weight of Blackbird was almost double that of Sophie, the percentage values of units per 100 pounds of empty body weight are approximately half the corresponding percentage values based on actual units of weight or measure, as shown in Table 4. The values in the seventh column range from 17.7 to 130.8 per cent. The table shows also that the weight of body part per 100 pounds of empty body weight is greater for Blackbird than for Sophie in only two instances—total weight of abdominal fat and weight of thyroid.

## MAMMARY GLAND

### ANTE-MORTEM EXAMINATION

A comparison of the external and internal udder structure of two cows specialized along such widely different lines is of particular

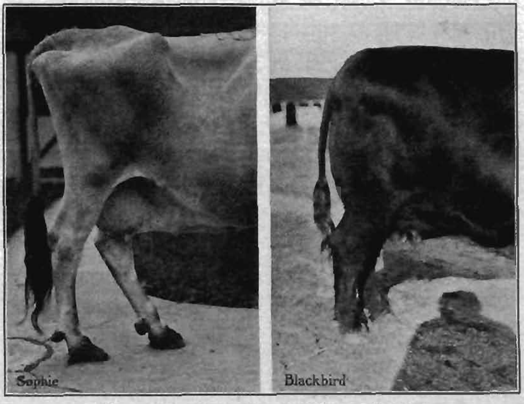


FIG. 6.—Side views of udders of Sophie and Blackbird

interest. Figures 3, 6, and 7 show external views of the udder of each cow. Some of the differences in appearance can be attributed to the season of the year and to the length of the nonlactating period. Sophie was photographed in midsummer, whereas Blackbird was photographed in midwinter, when her coat was heavy and shaggy. As previously stated, Sophie had been nonlactating for 3 or 4 months, whereas Blackbird had been dry for 25 months.

Figures 3, 6, and 7 indicate that Sophie's udder was remarkably loose and free of tissue, and that Blackbird's was more compact, more closely attached, and of much greater width and less depth. Detailed observations recorded a short time before the death of each cow showed that Sophie's udder was looser and more yielding and

that it contained considerably less total tissue. Blackbird's udder was described as fatty, yet the ante-mortem examination failed to differentiate completely between the fat and the mammary tissue or to indicate the relatively small quantity of mammary tissue in Blackbird's udder as revealed so emphatically in subsequent sectioning of the gland. Ante-mortem examination indicated also that Sophie had less distinctly separated but narrower halves and poorer attachment of gland tissue to abdominal wall. The tissue in Sophie's

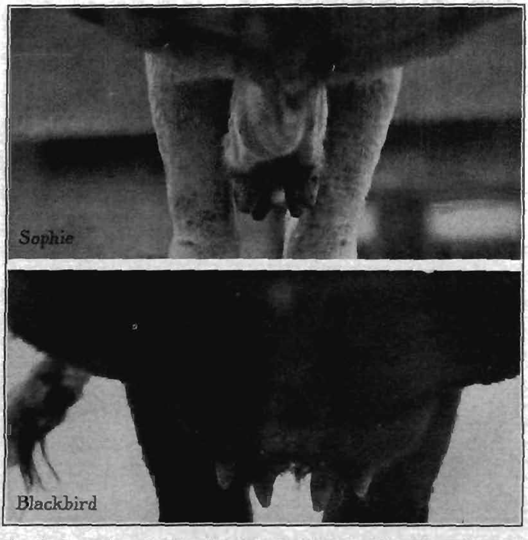


FIG. 7.—Front view of udders of Sophie and Blackbird. These photographs were taken with the camera resting on the ground and the lens directed upward and backward between the forelegs

udder appeared to be much harder and much more coarsely and harshly fibrous than that of Blackbird, which was more stringy. Sophie had greatly superior veins on udder and abdomen and larger milk wells, and the skin covering her udder was thinner, less mellow, and more flexible than that of Blackbird.

POST-MORTEM EXAMINATION OF INTERNAL STRUCTURE

In preparing the udder for the study of its gross anatomy, formalin was pumped through the teat canals into the secretory sys-

tem. Unfortunately, the quantity accommodated by Sophie's udder was not measured, but the average volume of fluid accommodated by seven nonlactating udders of dairy cows has been found to be equivalent to 25.8 pounds of milk. The udder of Blackbird, however, held only the equivalent of 8.22 pounds of milk.

The gross anatomy of the two udders is indicated by Figures 8 to 11, which are of approximately the same relative proportion and which show vertical transverse sections of the udders. The udder of Sophie had gland tissue over practically its entire area in both front and rear quarters (figs. 8 and 10); whereas Blackbird's udder had in the rear quarter an area of gland tissue somewhat irregular and pointed in shape, about 5½ inches at its maximum height and 3 inches at its maximum width, and surrounded laterally and superiorally with solid fat (fig. 9). In the front quarter (fig. 11) the area of gland tissue extended for about 1½ inches along and just beneath the skin and had a maximum depth of about five-eighths inch. The gland tissue was little more than sufficient to inclose the duct or cistern, which was not more than one-fourth inch in diameter, horizontal in position, and approached the teat canal from the rear. The front of this section, which was only approximately three-fourths inch thick, was of solid fat and showed no trace of gland tissue. The relatively great deposition of fat in Blackbird's udder may have been influenced to some extent by her longer dry period. This is of interest, but the significant point about her udder is the extremely small quantity of gland tissue present. This could hardly have been caused by the length of dry period. Udders from dairy cows that had been dry for extended periods showed a distribution of the mammary tissue throughout almost all of the gland. The small quantity of secretory tissue in Blackbird's udder appears, therefore, to have been an inherent characteristic of the cow. It is obvious that the udder of Blackbird was extremely limited in capacity for milk production.

## SKELETON

### CLEANING AND MOUNTING

The skeleton of each cow has been cleaned and mounted.[3] The cleaning of the bones was accomplished by a chemical process, without boiling, with the result that the texture of the bones, all the finest and most delicate bony structures, and the cartilage were preserved without injury. Except for the head and limbs, each skeleton was prepared, without disarticulation, in four units: (1) The neck; (2) the entire thoracic cage, consisting of vertebrae, ribs, and sternum, which was preserved intact; (3) the lumbar and pelvic portions; and (4) the tail. The hyoid also was preserved. The skeleton of each cow was mounted without significant alteration of shape or position of any bone, according to detailed measurements of the cow made before death. The methods employed have resulted in skeletons

[3] The skeleton work was done by C. E. Mirguet, an expert osteologist connected with the Smithsonian Institution in Washington, D. C.

FIG. 8.—Vertical transverse section through the two rear quarters of Sophie's udder

FIG. 9.—Vertical transverse section through one rear quarter of Blackbird's udder

FIG. 10.—Vertical transverse section through the two front quarters of Sophie's udder

FIG. 11.—Vertical transverse section through one front quarter of Blackbird's udder

which are considered unusually natural in shape and true to life. The two skeletons are illustrated in Figures 12, 13, and 14.

### COMPARISONS OF MEASUREMENTS

The two skeletons have been measured in detail. Since the position of the bones of the feet and legs, particularly those of the

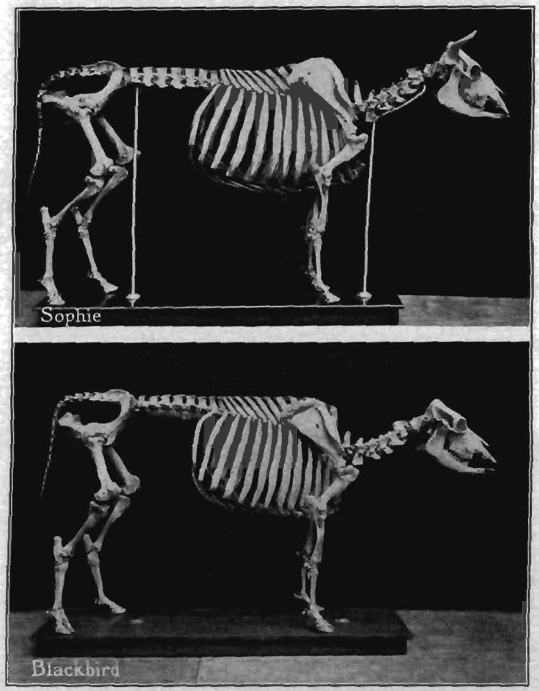


FIG. 12.—Side views of skeletons of Sophie and Blackbird

thoracic limb, are subject to considerable variation, few measurements were made which were based on their position, and relatively little significance can be attached to them except as each bone is considered as a unit.

In order to show graphically the differences in the shape of the

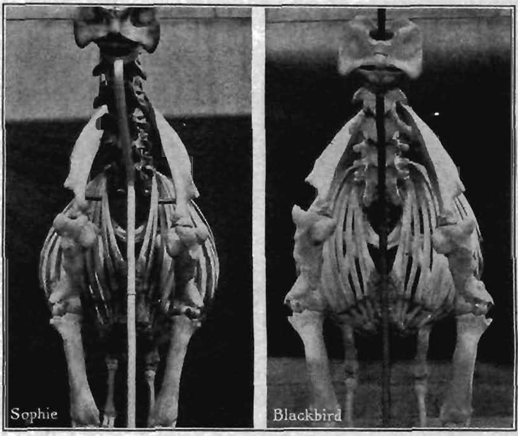


FIG. 13.—Front views of skeletons of Sophie and Blackbird

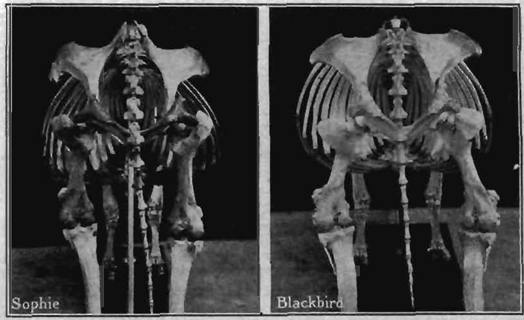


FIG. 14.—Rear views of skeletons of Sophie and Blackbird

chest and paunch have been prepared. Figure 15 shows the fore-chest contours of the two cows, and Figure 16 shows the contours through the paunch. Obviously the paunch contours could not be completed since the extremities of the ribs do not meet.

The fore-chest contours of the two cows are distinctly different in shape. The contour of Sophie is narrower but deeper than that of Blackbird. The areas, however, are almost identical, being 1,439 sq. cm. for Sophie and 1,418 sq. cm. for Blackbird. At the customary plane for taking contours of the paunch, the rear ribs of Black-

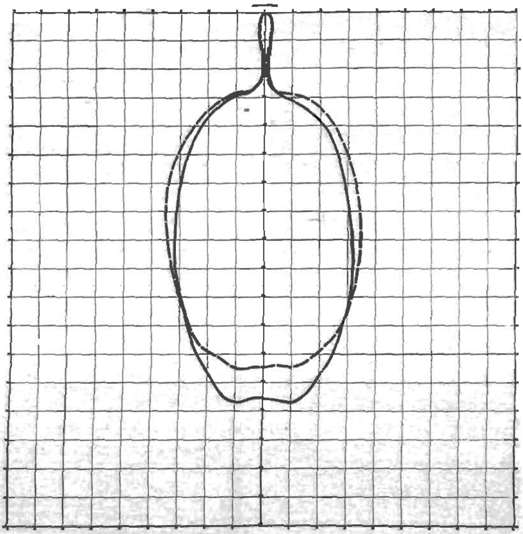

FIG. 15.—External contours of fore chest of skeleton. Solid line represents the contour of Sophie; broken line that of Blackbird

bird are more highly arched (greater spring of rib), whereas Sophie's ribs are straighter and extend considerably lower. By drawing a straight line connecting the rib extremities for each cow, the following contour areas of paunch were determined: for Sophie, 2,396 sq. cm.; for Blackbird, 2,107 sq. cm. The bony cages of the two cows differ greatly in shape. The cross-section areas at the fore chest are similar, but the cross-section area at the paunch is distinctly smaller for Blackbird than for Sophie. The area for Blackbird is 98.5 per cent of that of Sophie at the fore chest but only 87.9 per cent at the paunch.

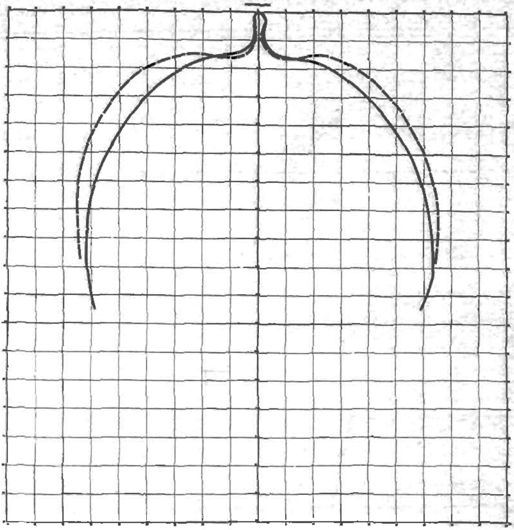

FIG. 16.—External contours of paunch of skeleton. Solid line represents the contour of Sophie; broken line that of Blackbird

The actual skeletal measurements of Sophie and Blackbird and their relative values, expressed in percentage of Sophie's measurements, are shown in Table 5.

TABLE 5.—*Detailed skeletal measurements of Sophie and Blackbird*

| Item | Sophie | Blackbird | Relation of Blackbird's data to those of Sophie |
|---|---|---|---|
| | *Cm.* | *Cm.* | *Per cent* |
| Height at top of highest thoracic spinous process | 120.00 | 113.75 | 94.8 |
| Height at highest point on sacrum | 121.25 | 117.75 | 97.1 |
| Height at top of hip points | 115.75 | 113.63 | 98.2 |
| Height at top of pin bones | 106.25 | 105.50 | 99.3 |
| Length between bearing surfaces: | | | |
| Bones of thoracic limb— | | | |
| Scapula | 37.00 | 34.00 | 91.9 |
| Humerus | 27.00 | 25.00 | 92.6 |
| Radius | 28.00 | 26.00 | 92.9 |
| Metacarpus | 20.50 | 19.00 | 92.7 |
| Total | 112.50 | 104.00 | ........ |
| Average | 28.13 | 26.00 | 92.4 |

TABLE 5.—*Detailed skeletal measurements of Sophie and Blackbird*—Continued

| Item | Sophie | Blackbird | Relation of Blackbird's data to those of Sophie |
|---|---|---|---|
| Length between bearing surfaces: | | | |
| *Bones of pelvic limb*— | *Cm.* | *Cm.* | *Per cent* |
| Femur | 35.50 | 34.00 | 95.8 |
| Tibia | 33.50 | 31.00 | 92.5 |
| Metatarsus | 23.00 | 23.00 | 100.0 |
| Total | 92.00 | 88.00 | |
| Average | 30.67 | 29.33 | 95.7 |
| Height at poll | 129.00 | 111.50 | 86.4 |
| Length, poll to third thoracic process | 71.00 | 64.00 | 90.1 |
| *Length, third thoracic process to point on spine between hips* | 89.50 | 89.00 | 99.4 |
| Length, point on spine between hips to rear of pin bones | 47.00 | 41.00 | 87.2 |
| *Length, third thoracic process to rear of pin bones* | 136.50 | 130.00 | 95.2 |
| Total length, poll to rear of pin bones | 207.50 | 194.00 | 93.5 |
| *Sway of back* | 5.00 | 2.50 | 50.0 |
| Width of fore chest (outside, sixth rib) | 33.25 | 33.75 | 101.5 |
| *Width of rear chest (outside, crossing center tenth rib)* | 55.00 | 52.50 | 95.5 |
| Width of paunch (outside, crossing center thirteenth rib) | 62.50 | 62.50 | 100.0 |
| *Depth of fore chest (plane of sixth rib)* | 68.50 | 62.25 | 90.9 |
| Maximum lateral width of thoracic cavity at anterior edge of each *rib:* | | | |
| 1 | 9.50 | 9.50 | 100.0 |
| 2 | 11.50 | 11.00 | 95.7 |
| 3 | 15.50 | 15.00 | 96.8 |
| 4 | 19.50 | 20.50 | 105.1 |
| 5 | 23.50 | 25.50 | 108.5 |
| 6 | 27.50 | 29.50 | 107.3 |
| 7 | 33.00 | 34.00 | 103.0 |
| 8 | 41.50 | 41.00 | 98.8 |
| 9 | 49.00 | 46.00 | 93.9 |
| 10 | 55.00 | 50.50 | 91.8 |
| 11 | 60.00 | 56.00 | 93.3 |
| 12 | 62.00 | 60.50 | 97.6 |
| 13 | 62.50 | 63.00 | 100.8 |
| Average | 36.15 | 35.54 | 98.3 |
| Vertical depth from ventral center of each thoracic vertebra to *sternum or to a horizontal line across the lower extremity of the* thoracic cage at the eighth to thirteenth vertebrae: | | | |
| 1 | 26.00 | 23.00 | 88.5 |
| 2 | 31.00 | 27.00 | 87.1 |
| 3 | 34.00 | 30.00 | 88.2 |
| 4 | 38.00 | 33.50 | 88.2 |
| 5 | 41.50 | 35.50 | 85.5 |
| 6 | 44.50 | 38.00 | 85.4 |
| 7 | 49.00 | 40.50 | 82.7 |
| 8 | 47.00 | 42.00 | 89.4 |
| 9 | 45.00 | 42.50 | 94.4 |
| 10 | 44.50 | 43.00 | 96.6 |
| 11 | 45.00 | 42.50 | 94.4 |
| 12 | 43.00 | 41.00 | 95.3 |
| 13 | 41.00 | 39.50 | 96.3 |
| Average | 40.73 | 36.77 | 90.3 |
| *Length, center of anterior edge of first rib to junction of thoracic* and lumbar vertebrae (length of thoracic cavity) | 76.00 | 72.50 | 95.4 |
| *Center axes, anterior aperture of thoracic cage:* | | | |
| Lateral | 8.00 | 8.00 | 100.0 |
| *Vertical* | 18.50 | 18.00 | 97.3 |
| Contour or cross-section area at anterior aperture of thoracic cage | 172.90 | 151.50 | 87.6 |
| *Contour area of thoracic cage (inside) at seventh rib* | 1,363.60 | 1,268.50 | 93.0 |
| Contour area of thoracic cage (inside) at thirteenth rib | 2,135.70 | 1,985.50 | 93.0 |
| *Height at anterior dorsal point of sternum (ventral point of anterior* aperture of thoracic cage) | 72.00 | 64.00 | 88.9 |
| *Height at dorsal median posterior point on sternum between attach-* ment of eighth ribs | 52.50 | 53.50 | 101.9 |
| *Length of sternum between above points* | 40.00 | 34.50 | 86.3 |
| Angle of sternum made with the horizontal | ([a]) | ([a]) | 60.7 |
| *Length of thoracic cage measured on spine (cervical-thoracic to* thoracic-lumbar junctions) | 76.00 | 71.00 | 93.4 |
| A*verage length each thoracic vertebra (divide above length by 13)* | 5.85 | 5.46 | 93.3 |
| Length of loin measured on spine (thoracic-lumbar to lumbar-sacral *junctions)* | 41.00 | 37.50 | 91.5 |
| Average length each lumbar vertebra (divide above length by 6) | 6.83 | 6.25 | 91.5 |

[a] Sophie, 29° 11′; Blackbird, 17° 43′.

TABLE 5.—*Detailed skeletal measurements of Sophie and Blackbird*—Continued

| Item | Sophie | Blackbird | Relation of Blackbird's data to those of Sophie |
|---|---|---|---|
| Length of spinous process of each thoracic vertebra: [b] | *Cm.* | *Cm.* | *Per cent.* |
| 1 | 25.00 | 22.00 | 88.0 |
| 2 | 25.00 | 22.00 | 88.0 |
| 3 | 24.50 | 22.00 | 89.8 |
| 4 | 23.50 | 21.00 | 89.4 |
| 5 | 21.50 | 19.50 | 90.7 |
| 6 | 20.50 | 19.00 | 92.7 |
| 7 | 20.00 | 18.00 | 90.0 |
| 8 | 18.50 | 17.00 | 91.9 |
| 9 | 17.00 | 16.00 | 94.1 |
| 10 | 14.50 | 14.00 | 96.6 |
| 11 | 12.00 | 12.00 | 100.0 |
| 12 | 9.00 | 9.00 | 100.0 |
| 13 | 7.50 | 7.50 | 100.0 |
| Average | 18.35 | 16.85 | 91.8 |
| Length of spinous process of each lumbar vertebra: | | | |
| 1 | 6.50 | 6.50 | 100.0 |
| 2 | 6.00 | 6.00 | 100.0 |
| 3 | 5.50 | 6.00 | 109.1 |
| 4 | 5.50 | 5.00 | 90.9 |
| 5 | 5.00 | 4.50 | 90.0 |
| 6 | 4.50 | 4.50 | 100.0 |
| Average | 5.50 | 5.42 | 98.5 |
| Width of each rib, 6 inches from its lowest ossified point (average of right and left): | | | |
| 1 | 2.13 | 2.32 | 108.9 |
| 2 | 2.42 | 2.31 | 95.5 |
| 3 | 3.31 | 2.92 | 88.2 |
| 4 | 4.42 | 3.88 | 87.8 |
| 5 | 5.05 | 4.35 | 86.1 |
| 6 | 5.23 | 4.47 | 85.5 |
| 7 | 5.81 | 4.93 | 84.9 |
| 8 | 5.41 | 4.54 | 83.9 |
| 9 | 4.92 | 4.15 | 84.3 |
| 10 | 4.69 | 3.66 | 78.0 |
| 11 | 3.96 | 3.45 | 87.1 |
| 12 | 3.19 | 2.48 | 77.7 |
| 13 | 3.29 | 2.20 | 66.9 |
| Total | 53.83 | 45.66 | ---------- |
| Average | 4.14 | 3.51 | 84.8 |
| Length of each rib, from vertebral attachment to lowest ossified point (average of right and left): | | | |
| 1 | 27.00 | 26.50 | 98.1 |
| 2 | 32.00 | 30.75 | 96.1 |
| 3 | 36.00 | 35.50 | 98.6 |
| 4 | 39.25 | 39.25 | 100.0 |
| 5 | 43.75 | 44.50 | 101.7 |
| 6 | 48.00 | 48.00 | 100.0 |
| 7 | 52.50 | 52.00 | 99.0 |
| 8 | 55.25 | 55.25 | 100.0 |
| 9 | 55.25 | 54.25 | 98.2 |
| 10 | 55.25 | 54.00 | 97.7 |
| 11 | 54.00 | 53.00 | 98.1 |
| 12 | 52.25 | 51.50 | 98.6 |
| 13 | 48.50 | 46.50 | 95.9 |
| Average | 46.08 | 45.46 | 98.7 |
| Width of intercostal spaces (spaces between ribs) approximately 6 inches from lowest ossified point: | | | |
| 1 | 1.89 | 1.97 | 104.2 |
| 2 | 2.15 | 2.55 | 118.6 |
| 3 | 1.96 | 2.41 | 123.0 |
| 4 | 1.80 | 1.97 | 109.4 |
| 5 | 1.80 | 1.71 | 95.0 |
| 6 | 2.76 | 2.53 | 91.7 |
| 7 | 1.30 | 2.00 | 153.8 |
| 8 | 3.75 | 3.05 | 81.3 |
| 9 | 4.51 | 3.58 | 79.4 |
| 10 | 4.78 | 4.37 | 91.4 |
| 11 | 4.92 | 5.03 | 102.2 |
| 12 | 5.07 | 5.18 | 102.2 |
| Total | 36.69 | 36.35 | ---------- |
| Average | 3.06 | 3.03 | 99.1 |

[b] Those of Sophie were set at extreme angle. Those of Blackbird were much more nearly vertical.

TABLE 5.—*Detailed skeletal measurements of Sophie and Blackbird*—Continued

| Item | Sophie | Blackbird | Relation of Blackbird's data to those of Sophie |
|---|---|---|---|
| Diameter of foramina of thoracic vertebrae (intervertebral and intravertebral): | *Cm.* | *Cm.* | *Per cent* |
| 1 | 1.22 | 1.25 | 102.5 |
| 2 | 1.16 | .57 | 49.1 |
| 3 | 1.21 | .48 | 39.7 |
| 4 | 1.05 | .61 | 58.1 |
| 5 | .94 | .83 | 88.3 |
| 6 | .92 | .55 | 59.8 |
| 7 | .94 | .70 | 74.5 |
| 8 | .87 | .71 | 81.6 |
| 9 | .98 | .80 | 81.6 |
| 10 | 1.10 | .76 | 69.1 |
| 11 | .84 | .68 | 81.0 |
| 12 | .74 | .64 | 86.5 |
| 13 | 2.94 | .78 | 26.5 |
| Average | 1.15 | .72 | 62.8 |
| Diameter of foramina of lumbar vertebrae (intervertebral and intravertebral): | | | |
| 1 | 2.20 | 1.28 | 58.2 |
| 2 [c] | **2.55** | **1.68** | **65.9** |
| 3 | 2.79 | 1.91 | 68.5 |
| 4 | 2.83 | 2.44 | 86.2 |
| 5 | 2.86 | 2.32 | 81.1 |
| 6 | 2.24 | 1.97 | 87.9 |
| Average | 2.58 | 1.93 | 75.0 |
| Length of loin, from center of hip to vertebral attachment of thirteenth rib | 45.00 | 42.00 | 93.3 |
| *Width of loin:* | | | |
| Third lumbar | 29.00 | 29.75 | 102.6 |
| Fourth lumbar | 30.25 | 32.50 | 107.4 |
| Average | 29.63 | 31.13 | 105.1 |
| Width of hips (outside extremity) | 46.50 | 47.25 | 101.6 |
| Width of thurls (outside extremity) | 40.50 | 39.25 | 96.9 |
| Width of pin bones (outside extremity) | 27.50 | 23.75 | 86.4 |
| Length of rump, top of hip to top of pin bone | 40.00 | 35.00 | 87.5 |
| Angle of rump | ([d]) | ([d]) | 97.8 |
| Angle of floor of pelvis | ([e]) | ([e]) | 124.5 |
| Angle of pelvic aperture | ([f]) | ([f]) | 106.4 |
| Length of pelvic floor | 17.50 | 17.00 | 97.1 |
| Center axes of pelvic aperture: | | | |
| Lateral | 25.00 | 24.50 | 98.0 |
| Longitudinal | 17.20 | 15.50 | 90.1 |
| Contour area of pelvic aperture | 392.00 | 350.90 | 89.5 |
| Width between top points of pin bones | 20.00 | 17.00 | 85.0 |
| Width of pelvis immediately above center of acetabulum | 17.75 | 16.50 | 93.0 |
| Width of forehead | 14.25 | 15.75 | 110.5 |
| Width across eyes | 20.75 | 22.25 | 107.2 |
| Length from poll to tip of nose | 47.00 | 45.50 | 96.8 |
| Greatest depth at angle of jaw | 26.00 | 24.25 | 93.3 |
| *Measurements of muzzle:* | | | |
| Outside width of premaxillae (nasal processes)— | | | |
| At narrowest point corresponding to corner of mouth | 7.66 | 7.64 | 99.7 |
| Near anterior extremity, corresponding to greatest width of prehensile pad | 8.28 | 8.50 | 102.7 |
| Outside width of mandible (lower jaw)— | | | |
| At narrowest point, corresponding to corner of mouth | 3.50 | 4.05 | 115.7 |
| Near anterior extremity, corresponding to lateral limits of incisor teeth | 7.74 | 7.45 | 96.3 |
| Inside diameters of nasal passage— | | | |
| Lateral diameter | 6.72 | 6.42 | 95.5 |
| Depth from roof to floor | 6.05 | 5.65 | 93.4 |
| Measurements of bones of thoracic limb (scapula not included). Center of shaft of: | | | |
| Humerus— | | | |
| Circumference | 14.00 | 15.00 | 107.1 |
| Lateral diameter | 3.92 | 4.32 | 110.2 |
| Anterior-posterior diameter | 4.87 | 5.17 | 106.2 |
| Radius— | | | |
| Circumference | 13.00 | 14.50 | 111.5 |
| Lateral diameter | 4.64 | 5.47 | 117.9 |
| Anterior-posterior diameter | 3.17 | 3.50 | 110.4 |

[c] Opening for nerve branch that goes to udder.
[d] Sophie 13° 44′; Blackbird 13° 26′.
[e] Sophie [illegible]° 36′; Blackbird 20° 40′.
[f] Sophie 38° 19′; Blackbird 40° [illegible]′.

TABLE 5.—*Detailed skeletal measurements of Sophie and Blackbird*—Continued

| Item | Sophie | Blackbird | Relation of Blackbird's data to those of Sophie |
|---|---|---|---|
| Measurements of bones of thoracic limb (scapula not included)—Continued. | | | |
| Center of shaft of:—Continued. | | | |
| Metacarpus— | *Cm.* | *Cm.* | *Per cent* |
| Circumference | 9.50 | 10.75 | 113.2 |
| Lateral diameter | 3.30 | 3.87 | 117.3 |
| Anterior-posterior diameter | 2.29 | 2.54 | 110.9 |
| Average | 6.52 | 7.24 | 111.0 |
| Measurements of bones of pelvic limb. Center of shaft of: | | | |
| Femur— | | | |
| Circumference | 12.50 | 13.50 | 108.0 |
| Lateral diameter | 3.53 | 3.85 | 109.1 |
| Anterior-posterior diameter | 4.30 | 4.64 | 107.9 |
| Tibia— | | | |
| Circumference | 11.50 | 13.00 | 113.0 |
| Lateral diameter | 4.10 | 4.96 | 121.0 |
| Anterior-posterior diameter | 2.93 | 2.86 | 97.6 |
| Metatarsus— | | | |
| Circumference | 9.50 | 11.00 | 115.8 |
| Lateral diameter | 2.78 | 3.20 | 115.1 |
| Anterior-posterior diameter | 2.90 | 3.53 | 121.7 |
| Average | 6.00 | 6.73 | 112.0 |

The skeleton of Sophie is slightly taller and about 6 or 7 per cent longer than that of Blackbird. The head and front quarters of Blackbird are relatively low. The total length of the bones of the front leg of Blackbird is only 92.4 per cent of that of Sophie, whereas the length of the bones of the hind leg is 95.7 per cent as great. Sophie has a greater dip or sway of back than Blackbird.

Blackbird is slightly greater than Sophie in external width of fore chest, narrower in rear chest, the same in width of paunch, but decidedly less in depth of fore chest. Measurements of the internal widths of thoracic cavity taken at the anterior edge of each rib show on an average nearly the same values for each cow, although Blackbird is very slightly wider than Sophie in the front half and very slightly narrower in the rear half of the thorax. The internal vertical depths from the center of each vertebra to the sternum show that Blackbird is consistently shallower, averaging only 90.3 per cent the depth of Sophie. The length of thoracic cavity also is slightly less for Blackbird than for Sophie. The anterior aperture of the thoracic cavity is of nearly the same dimensions for each cow, but the contour areas of the openings are decidedly less for Blackbird than for Sophie. The areas of the inside contours across the seventh and thirteenth ribs have the same relationship for the two cows, being in each case 93 per cent as great for Blackbird as for Sophie. Blackbird's sternum is lower in front, very slightly higher at the rear and much shorter. It has, therefore, a very much smaller angle of inclination from the horizontal, indicating that in skeletal structure she had less vertical wedge shape than Sophie. On the contrary, the widths of fore chest, rear chest, and paunch indicate that in skeletal structure the two cows exhibited almost exactly the same degree of wedge shape laterally. Heavy fleshing in the region of the shoulders and fore chest undoubtedly was responsible for the fact that Blackbird when living showed relatively very little of the

lateral wedge shape externally. Blackbird's thoracic cavity is shorter, and the average length of her thoracic vertebrae is correspondingly less than that of Sophie. Similarly, the lengths of the lumbar region and of each lumbar vertebra of Blackbird are considerably shorter than those of Sophie.

A marked difference exists between the spinous processes of the thoracic vertebrae of the two cows. Those of Sophie incline backward at a distinct angle, whereas those of Blackbird are much more nearly vertical. The angle of inclination of these processes was not measured, but the differences are clearly indicated in Figures 17 and 18. In length, the processes of Sophie are considerably greater than those of Blackbird. This difference is distinctly noticeable in the anterior thoracic vertebrae but diminishes steadily as the more posterior vertebrae are approached, the eleventh, twelfth, and thirteenth being of equal length in both cows. On an average the processes of Blackbird are 91.8 per cent as long as those of Sophie. The lumbar processes of both cows are similar in shape and in length.

One outstanding difference between the two cows is the width of ribs measured 6 inches above the lowest ossified point. Except for the first rib those of Sophie are in every case wider than those of Blackbird. The difference increases rather steadily from the second to the thirteenth rib. On an average those of Blackbird are 84.8 per cent as wide as those of Sophie.

The length of ribs is approximately the same for each cow, although Blackbird's are more arched in the upper or dorsal portion. The width of spaces between ribs varies considerably at certain points, but on an average they are almost identical. The greater width of each rib of Sophie with equal intercostal spaces gives her a considerably greater length of thoracic cavity in the region of the lower part of the rib.

Judges of dairy cattle are inclined to attach considerable importance to the openness of conformation or the width of the spaces between ribs, spinous processes, and vertebrae, believing that such openness allows more space for the nerves to pass out through the spine from the spinal cord. According to Sisson[4] "The notches of two adjacent vertebrae form intervertebral foramina (*Foramina intervertebralia*) for the passage of the spinal nerves and vessels; in some vertebrae, however, there are complete foramina instead of notches." Attention should be called to the fact that there are more intravertebral than intervertebral foramina in these skeletons. The intravertebral foramina appear near the center of the vertebrae and could hardly be associated with the width of spaces between the tops of the spinous processes. Furthermore, the intervertebral foramina are nearly all in the region of the lumbar vertebrae where the distances between the tops of the processes are not readily determined by examining the living animal. It appears, therefore, that judgment of the width of spaces between spinous processes in the living animal is not particularly significant of the freedom of passage of nerves from the spinal cord. These foramina, whether intervertebral or intravertebral, have been measured as accurately as possible.

[4] SISSON, S. THE ANATOMY OF THE DOMESTIC ANIMALS. Ed. 2, p. 26. Philadelphia and London, W. B. Saunders Co. 1914.

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Because of their location and position, measurement of some of them was difficult. Most of them are nearly round, but some are irregular in shape. The measurements recorded are the greatest transverse diameters of the openings. In a few cases the vertebrae show both intervertebral and intravertebral foramina. In a few instances, especially in the lumbar region, the foramina are divided either by cartilage or bone into two parts. Wherever a vertebra shows two foramina or one divided into two parts, both have been measured and the total of the two diameters recorded for that vertebra. The foramina of Blackbird are very much smaller than those of Sophie. On an average the thoracic foramina of Blackbird are 62.8 per cent as large as those of Sophie. The corresponding relative size for lumbar foramina is 75 per cent. The lumbar and thoracic vertebrae of Sophie and Blackbird are shown in Figures 17 and 18.

Smith [5] states:

> The mammary gland is innervated in quadrupeds (in addition to the ileo-inguinal nerve distributed to the skin) by the external spermatic nerve. This nerve originates from the lumbar portion of the spinal cord and passes out between the greater and lesser psoas muscles, dividing in the pelvis into three branches, of which one is distributed to the abdominal muscles, while the other two leave the abdominal cavity through the femoral ring accompanying the crural artery, and then, following the course of the external pudic artery, are distributed to the mammary gland.

Sisson [6] specifically describes the origin of this nerve as follows:

> It (one of the branches of the second lumbar nerve) joins a branch of the external spermatic nerve, and the trunk so formed descends the inguinal canal, to be distributed to the external genital organs and the surrounding skin in the inguinal region. * * * The external spermatic nerve (*N. spermaticus externus*, third lumbar nerve) passes backward in the substance of the psoas minor and divides into two branches.[7]

One of these branches emerges behind the circumflex iliac vessels and—

> runs lateral to and parallel with the external iliac artery and descends in the medial part of the inguinal canal. It emerges at the external ring with the external pudic artery and ramifies in the external genital organs and the skin of the inguinal region. * * * The origin and disposition of some of the foregoing nerves are variable. In some cases the ilio-inguinal nerve ends in the psoas major, and appears then to be absent. The mode of formation of the inguinal nerves is inconstant.

It appears that the nerves which control the udder leave the spinal cord and pass through the foramina between the second and third lumbar vertebrae. The diameters of these foramina are 2.55 cm. for Sophie and 1.68 cm. for Blackbird, as shown in Table 5. The foramina of Blackbird, therefore, have diameters only 65.9 per cent as great as those of Sophie. The significance of these diameters, however, may be subject to speculation.

Blackbird has a shorter but slightly wider loin than Sophie, and her lateral processes turn upward instead of downward at the ends as in the case of Sophie. The width of hips is very slightly greater, whereas width of thurls, width of pin bones, and length of rump are less for Blackbird than for Sophie.

[5] SMITH, R. M. THE PHYSIOLOGY OF THE DOMESTIC ANIMALS. p. 629. Philadelphia and London, F. A. Davis. 1889.

[6] SISSON, S. Op. cit., pp. 822–823.

[7] According to the diagram on p. 822 of Sisson the external spermatic nerve appears to emerge between the second and third lumbar vertebrae.

In angle of rump the two skeletons are similar. This may appear to be inconsistent, since the angle of rump on the living animal was somewhat less for Blackbird than for Sophie. Part of this discrepancy is due to the difficulty experienced in measuring the body

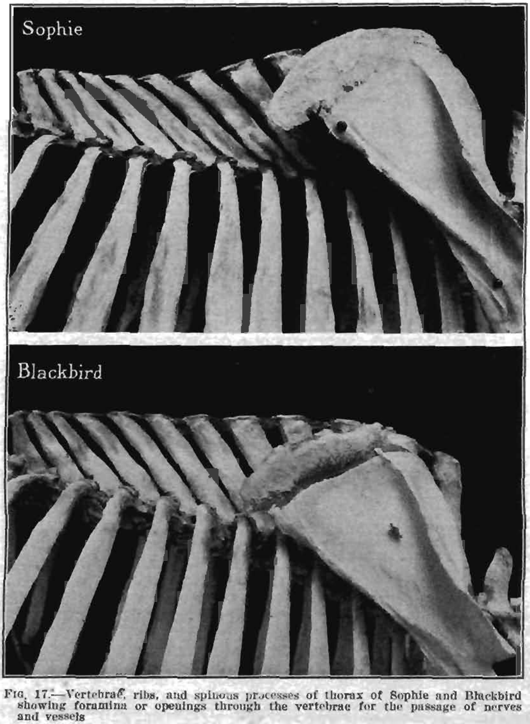


FIG. 17.—Vertebræ, ribs, and spinous processes of thorax of Sophie and Blackbird showing foramina or openings through the vertebrae for the passage of nerves and vessels

of Blackbird because of the amount of subcutaneous fat over her hips and pin bones. The skeleton also shrinks in drying, which results in a tendency for the spine to become slightly arched. A very slight difference in the amount of arching may affect the angle of inclination of the rump or pelvis. This was carefully guarded against but may not have been entirely avoided. The shrinkage of the skeleton

also accounts for some of the reductions in skeletal lengths as compared with similar measurements of the living form.

The floor of the pelvis tends to incline upward toward the rear. The angle is considerably greater for Blackbird than for Sophie. The angle which the plane of the pelvic aperture, or anterior opening of the pelvis, makes with a horizontal is not greatly different for

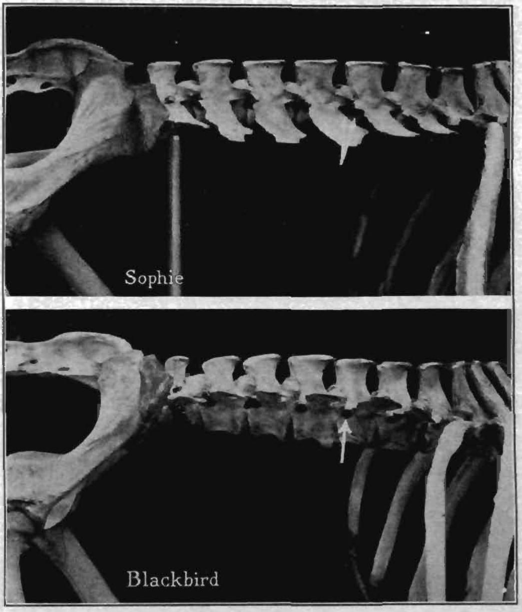


FIG. 18.—Lumbar vertebrae and spinous processes of Sophie and Blackbird showing intravertebral and intervertebral foramina. Arrows indicate foramina which permit passage of nerve which innervates the mammary gland

the two cows. The length of pelvic floor is approximately the same for both cows. The axis of the pelvic aperture of Blackbird is about the same laterally as that of Sophie but is considerably less longitudinally. The contour or cross-section area of the pelvic aperture is distinctly greater for Sophie than for Blackbird. In width of pelvis both across the top points of the pin bones and across the center of the acetabulum, the measurements are greater for Sophie than for Blackbird. It appears that Sophie had a greater space for

delivery of fetus than did Blackbird. In this connection it is of interest to note the birth weight of Jersey and Aberdeen Angus calves. The average birth weight of 83 Jersey calves recorded at the Beltsville, Md., station is 57.3 pounds. Assembled data, furnished by four experiment stations,[8] indicate an average birth weight of 69 pounds for 424 Aberdeen Angus calves.

Blackbird is wider in the forehead and across the eyes, whereas Sophie is longer from poll to tip of nose. Sophie also is deeper through the maximum depth of jaw. The widths of nasal processes are similar for the two cows. The widths of mandible are nearly the same, that of Sophie being slightly greater at one point of measurement and slightly less at the other. The inside diameters of the nasal passage, however, are both slightly greater for Sophie than for Blackbird. The muzzle measurements of the skeletons are strikingly similar. The circumference of muzzle of the two cows when living was 108.5 per cent as great for Blackbird as for Sophie.

The circumference, the lateral diameter, and the anterior-posterior diameter of the humerus, radius, metacarpus, femur, tibia, and metatarsus were measured. In all except 1 of the 18 measurements, the values are greater for Blackbird than for Sophie. The one exception is the anterior-posterior diameter of the tibia which, because of its shape, was particularly difficult to measure. The leg bones of Blackbird are distinctly heavier or greater in diameter than those of Sophie, not only in proportion to their length, but also in actual units of measurement.

## SUMMARY

### EXTERNAL FORM OF LIVING ANIMAL

Blackbird was in very high condition of flesh and had a deposition of subcutaneous fat as great as 9 cm. in thickness in some places. Sophie had very little body fat and weighed 638 pounds less than Blackbird.

Blackbird was slightly higher at the pin bones, of approximately the same height at the hips, but lower at the withers. On an average she was 98.8 per cent as tall as Sophie. She also was shorter in body than Sophie.

Blackbird was distinctly deeper in body and showed a far greater vertical wedge shape than Sophie. She was much wider but exhibited only about half as much lateral wedge shape as did Sophie. Body circumferences and contour or cross-section areas of fore chest and paunch were much greater for Blackbird than for Sophie, yet both measurements indicated greater body wedge shape for Sophie.

Blackbird's body surface area appeared to be about 20 per cent greater than that of Sophie.

The calculated volume of barrel was nearly 70 per cent greater for Blackbird than for Sophie.

Blackbird was wider in proportion to depth both at the fore chest and paunch, with resulting lower thoracic and abdominal indexes than those of Sophie.

[8] Acknowledgment is made for the assistance rendered by members of the animal husbandry departments of the Illinois, Mississippi, Nebraska, and Ohio experiment stations in furnishing these data.

Blackbird was slightly more nearly level in the rump than was Sophie. The influence of fat deposition on this point is speculative.

The legginess of Blackbird was approximately 87 per cent of that of Sophie.

Heaviness of bone, as judged by circumference of shin bone or metacarpus of the living animal, was considerably greater for Blackbird than for Sophie.

Blackbird had a slightly shorter head, wider forehead, and greater circumference of muzzle.

The greater height, greater length of body, and greater length of head are all indicative of greater "scale" for Sophie.

Only five of the measurements that are greater for Blackbird than for Sophie are more than 25 per cent in excess. In each of these five items, the marked difference between the two cows can be attributed largely to the heavy fleshing and fat deposition of Blackbird.

## INTERNAL ANATOMY

The empty body weight of Blackbird was 707.8 pounds, or 92.1 per cent greater than that of Sophie. As might be anticipated under these conditions, the weights of organs or body parts per 100 pounds of empty body weight were much lower for Blackbird than for Sophie.

The weights of kidneys and of adrenals were distinctly greater for Blackbird than for Sophie.

The weight of spleen was almost the same for both cows.

The weights of empty stomachs and of empty intestines were much less for Blackbird than for Sophie.

Blackbird had 181.71 feet of intestines as compared with 166.50 feet for Sophie. The intestinal lengths of Sophie and Blackbird are about intermediate to the range of intestine lengths obtained from a large group of cows.

An accurate weight of Sophie's lungs was not obtained. Blackbird's lungs appeared to be relatively low in actual weight and in weight per 100 pounds empty body weight when compared with similar data obtained from a large group of cows.

The weight and circumferences of heart were similar for both cows. Both were below the average heart weight obtained on a large number of cows. Furthermore, the weight of heart per 100 pounds of empty body weight was relatively low for Blackbird.

The weight of thyroid was very much greater for Blackbird than for Sophie. This can be attributed largely to the interlying of fat in the case of Blackbird.

Except for the weight of intestines, intestine contents, stomachs, stomach contents, heart, and one of the heart circumferences, all the weights and measurements given in Table 4 are greater for Blackbird than for Sophie. The difference in weight of heart is so small that it is negligible.

## MAMMARY GLAND

Externally, the udder of Blackbird, as compared with that of Sophie, was more compact and more closely attached with less looseness, greater width, and less depth. It appeared to have a greater total quantity of tissue which was more yielding and much

less coarsely and harshly fibrous than that of Sophie. Blackbird had relatively very inferior veins on udder and on abdomen and smaller and less distinct milk wells. The skin covering the udder of Blackbird was thicker, mellower, and less flexible than that of Sophie.

Internally, Sophie's udder had gland tissue over almost the entire area of each of the transverse sections into which it was cut. The rear quarter of Blackbird's udder had only a very small quantity of gland tissue surrounded by a heavy deposition of firm fat. Sections through the front quarter of Blackbird's udder showed little more than a duct or cistern, about a quarter of an inch in diameter and extending longitudinally to the front teat.

SKELETON

Blackbird is not so tall and is shorter in body than Sophie. Her leg bones are shorter and her head and front quarters are lower.

Measurements of the outside of the thoracic cage of the skeletons indicate that Blackbird is slightly wider in fore chest, narrower in rear chest, and of the same width of paunch as Sophie. She also is decidedly shallower in fore chest. The rear ribs of Blackbird are much more highly sprung or arched than those of Sophie.

The internal skeletal measurements of the thoracic cage show on an average almost the same widths for both cows. Blackbird, however, has decidedly less depth and somewhat less length of thorax. The inside contours at the seventh and at the thirteenth ribs are in each case 93 per cent as great for Blackbird as for Sophie. The anterior aperture of the thoracic cage is similar in dimensions for both cows but very much less in area for Blackbird than for Sophie.

Blackbird's sternum is much shorter, decidedly lower in front, and very slightly higher in the rear, giving her decidedly less of the vertical wedge shape. In lateral wedge shape, however, the two skeletons are almost identical, although in their living form, because of difference in fleshing, Sophie had almost twice as much lateral wedge shape as Blackbird.

Blackbird's thoracic vertebrae are shorter than Sophie's, and the spinous processes are shorter and much more nearly vertical. Her ribs are very much narrower but of about the same length as Sophie's, and the width between ribs averages almost the same for both cows.

Blackbird is shorter but wider in the loin and has shorter lumbar vertebrae. The lumbar spinous processes of both cows are approximately the same in shape and in length. The transverse lumbar processes of Blackbird incline upward, whereas those of Sophie are turned downward.

The diameters of thoracic foramina are only 62.8 per cent as great for Blackbird as for Sophie. The corresponding diameters of lumbar foramina are 75 per cent as great for Blackbird as for Sophie. The foramina which allow passage of the nerves which innervate the udder are 65.9 per cent as great in diameter for Blackbird as for Sophie.

Blackbird is very slightly wider at the hips but narrower at the thurls and pin bones. She is shorter in the rump with almost the same angle of rump as Sophie.

Blackbird's pelvis is narrower and slightly shorter on the floor. Both the pelvic floor and the plane of the pelvic aperture have greater angles of inclination than those of Sophie. The pelvic aperture, or anterior opening of the pelvis, is slightly narrower, distinctly shorter, and has a decidedly smaller area, allowing less space for delivery of the fetus, although average birth weights of Jersey and Aberdeen Angus calves are shown to be 57.3 and 69 pounds respectively.

Blackbird has a wider but slightly shorter head and a shallower jaw. The muzzles of the two cows are similar in width. Blackbird has a somewhat smaller nasal passage.

The leg bones of Blackbird are distinctly heavier, and greater in lateral and anterior-posterior diameter, both in actual measurements and in proportion to their length.

Obviously a comparison of large numbers of dairy and beef skeletons is at present impossible because of the limited material available. The foregoing data are presented to show the general differences between these two skeletons. It is not to be inferred that the same or similar differences would be found between all dairy and beef skeletons.

## GENERAL

In external form the two cows differed greatly.

In weight and size of internal organs, the differences were not sufficiently great to indicate significant differences in function.

In skeleton structure the two cows varied somewhat but were generally similar. This would indicate that the evolution of the dairy and beef types, which has been accomplished through breeding and selection, has not materially altered their skeletal structure, but rather that the difference in type is due to extreme fleshing on the one hand and to udder development and absence of fleshing on the other.

Aside from the external form, the most marked difference noted between the cows compared was the quantity of secretory tissue in their udders.

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# THE USEFULNESS OF CAPILLARY POTENTIAL TO SOIL-MOISTURE AND PLANT INVESTIGATORS[1]

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## INTRODUCTION

Soils literature contains numerous discussions of the problem of the movement of moisture in the soil and its availability to the plant. In a great many cases, however, the point of view is that of the experimentalist, and the possible advantages that may accrue from a consideration of the generalizations available in the literature of physics and chemistry are almost wholly overlooked.

One investigator, for example, discovers from his experiments that water evaporates more rapidly from a moist than from a dry soil; another discovers that the moisture tends to accumulate toward the rim of a sample in the centrifugal machine; still another finds that a wet clay will absorb moisture from a sand comparatively drier. Many examples of this character may be pointed out as results of experimentation purporting to represent contributions to scientific knowledge. By such experimental procedure and by careful analysis of the resulting data we may succeed anew in working out generalizations from which we may predict with some degree of certainty, qualitatively at least, the way in which soil water will move under certain conditions. If we are to profit by experience we must make these generalizations, but it is quite probable that in many cases such generalizations will be found to conform with those that are already known to the basic sciences.

It is at once obvious that a mixture of mineral fragments of numerous kinds in the presence of organic material and moisture constitutes a complicated system. Rainfall and evaporation, with seasonal and daily variations in the temperature, subject the soil surface to fluctuations so that, in general, the system must be regarded as dynamical, the principal "reactions" being a readjustment of the soil structure and a movement of the moisture. This paper is concerned with methods for studying the phenomena connected with this latter reaction.

Capillary and gravitational forces are always involved as factors determining the conditions of motion or of equilibrium of moisture in the soil. There is much evidence for believing that most soils are "wetted" by water, and hence the adhesive attraction of water molecules for soil grains and the cohesive attraction of one water molecule for another are suppressed to indirect relationship and need not enter into the analysis. Gravitational forces on the elemental

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[2] The author is deeply indebted to Prof. Willard Gardner for his kind assistance and encouragement. Appreciation is also expressed to Dr. D. S. Jennings for making available at various times soils and equipment of the soils department, and to Sterling J. Richards for assistance during the experimental work and in the preparation of this paper.

particles are measured by the masses of the particles themselves, so there remains the single somewhat obscure force of capillarity with which to deal.

By making use of potential functions physicists have developed a dynamical method which has materially aided in studying the flow of heat and electricity. If we adopt this method we can remove many of the difficulties in the field of soil moisture by using what is known as the capillary potential function.[3] This function is simply an application of the well-known energy-potential theory. Capillary potential differences have the same relation to the flow of moisture in soil as voltage differences have to the flow of electricity in wires, or as pressure differences have to the flow of water in pipes. This latter is a rather close analogy because the capillary potential at any given point in the water between soil grains is numerically equal to the hydrostatic pressure at that point.[5]

Definitions and discussions of the capillary potential, involving more or less mathematics, are already to be found in available literature, but since potential functions have not been extensively used by workers in the agricultural sciences it has been thought worth while to present a discussion of the capillary potential without the use of detailed mathematical analysis. To aid in making clear the nature of this function the characteristics of the electrostatic, gravitational, and pressure potentials are briefly reviewed. The close relation between the capillary potential and the pressure potential (which in water is numerically equal to the hydrostatic pressure) makes it possible to introduce the capillary function in terms of more commonly used quantities.

This paper also presents some experimental data which show the relation between capillary potential and moisture percentage for several different soils, and attention is called to some of the ways in which capillary potential may be used.

## DEFINITION AND CHARACTERISTICS OF POTENTIAL FUNCTIONS

### ELECTROSTATIC POTENTIAL

In general, it may be said that potential functions [6] are more or less artificial creations of the mind, defined and used because they are helpful in studying and accurately expressing the processes of nature. In dealing with electricity we have come to regard potential

[3] The capillary potential as a magnitude to be used in the study of soil moisture was first introduced and defined by Buckingham (*2*) [4] in 1906. The methods then known for measuring this magnitude were rather slow and of uncertain accuracy, so the function was of little experimental use. It is an interesting coincidence that in 1906, the same year Buckingham submitted his article, Livingston (*18*) developed apparatus, called by him autoirrigators, which could be used as a quantitative means of controlling the capillary potential in soil. However, there seems to have been no correlation established between autoirrigators and the Buckingham potential function until about 15 years later, when it was pointed out by Gardner (*7*) and his associates that porous clay equipment could be used to measure the value of this function.

[4] Reference is made by number (italic) to "Literature cited," p. 741.

[5] The capillary potential in water is numerically equal to the hydrostatic pressure only when the units used are such that the density of water is unity.

[6] In a singly connected, conservative force field the potential at any point is the amount of work required to move a unit mass from an arbitrarily chosen point of zero potential to the point in question. If $f$ as a vector is the externally exerted force on unit mass and $ds$ an infinitesimal vector along the path, then the potential at any point $B$ is, $W = \int_A^B f ds$ where $A$ is the arbitrarily chosen point of zero potential. If there is no force in the field the potential will be constant throughout.

In case more than one force field exists in a region the potential for each field and the potential due to the resultant field or total potential is defined by the above relation. If equilibrium obtains, the forces are balanced and the total potential will be constant throughout the region. The potential at any point is independent of the mass present and is the work that would be required to move unit mass from the point of zero potential to the point in question.

as indispensable. Because the term "potential" is commonly associated with electricity, and because the electrostatic potential is similar in so many ways to the potentials to be discussed in this paper, the characteristics of the electrostatic potential function are briefly reviewed.

If static electrical charges are accumulated at different places in a certain region there will be electrical forces exerted on other charges which are brought into that region and there is said to exist an electrostatic "force field." The field intensity, which is defined as the force on a unit positive charge, has a definite direction and magnitude at every point in the region. It is called a point function because every point in the region is characterized by the direction and magnitude of the field intensity at the point. Now, it is possible completely to represent this force field by means of another point function called potential. The potential is a function such that if its value is known for every point in the region then the direction and magnitude of the field force at any point can be calculated. The electrostatic potential at any given point is defined as the amount of work that must be done against the field forces in bringing a unit positive charge from some reference level to the point in question. The term "work," as here used, has its usual meaning. It is the product of a force times a distance. For example, if a force of 5 gm. moves a body a distance of 2 cm. in the direction of the force, then 10 gm. centimeters of work have been accomplished. Since potential is defined in terms of the work done in moving a unit charge in the force field, then the difference in potential between two points is simply the work required to move a unit charge from one point to the other. Hence, if the potential is known at two different points, then the average component of the field force acting on a unit charge in the direction of the line connecting the two points is simply the difference in potential divided by their distance apart, the force being directed from high to low potential. If we let $V$ stand for the electrostatic potential, then for every point in an electrostatic field $V$ will have a certain definite value. If $V$ is everywhere the same, then it requires no work to move a charge from one point to another and the electric field intensity must be zero, i. e., there are no forces acting. If, however, $V$ changes in value from point to point there will be a direction in which its space rate of change will be a maximum. This change in potential per unit of distance in the direction of the maximum rate of increase of potential is called the potential gradient and is designated by grad $V$. The field intensity $E$ is everywhere equal in magnitude and opposite in direction to the gradient of $V$, or

$$E = -\text{grad } V \tag{1}$$

This relation is especially important.

As we proceed, it should be noticed that there is a striking analogy to the electrostatic case between both the way in which the gravitational and pressure potentials are defined and the way in which the gravity and the pressure field force is related to the potential gradient.

## GRAVITATIONAL AND PRESSURE POTENTIALS

Bernouilli's equation, which is discussed in almost every college physics textbook, expresses the relation connecting the gravity

energy, the kinetic energy, and the pressure in a moving fluid.[7] It may be written as follows:

$$gh + p/\rho + \tfrac{1}{2}v^2 = K \qquad (2)$$

where, in the centimeter-gram-second system of units, $h$ is the height in centimeters of a point above a fixed level; $g$ is the acceleration of gravity, 980 cm. per second per second; $p$ is the pressure in the fluid at the point expressed in dynes per square centimeter (in the centimeter-gram-second system the dyne is the unit of force; 980 dynes = 1 gm.); $\rho$ is the density of the fluid in grams per cubic centimeter; $v$ is the velocity of the fluid at the point in centimeters per second; and $K$ is a constant.

We shall first consider systems which are at static equilibrium. Under this condition the velocity is zero and equation (2) becomes,

$$gh + p/\rho = K \qquad (3)$$

In applying this equation we shall deal only with the potential and force relations within the region occupied by the liquid. The first term is the expression for the gravitational potential at the point under consideration. It is the work, in dyne centimeters, that would have to be done against the gravity field force in order to raise 1 gm. of matter to a height $h$ centimeters above a gravity reference level. For the systems we shall here consider, the free flat liquid surface will be used as the reference level for the gravitational potential. Let the gravitational potential be designated by $\phi$. Then from (3) the value of $\phi$ at any point in the region is

$$\phi = gh \qquad (4)$$

where $h$ is the vertical distance of the point from the free flat water surface level. If the point is above this surface, then $h$ will be taken as a positive quantity. For points below the water surface, $h$ will be negative. (This convention as to the algebraic sign of $h$ will be used in subsequent formulas in which $h$ is used.)

Equation (4) shows that the gravitational potential is proportional to the vertical distance from the reference level and that it increases with the height. This means that vertically upward is the direction of the potential gradient. The gravity force per unit of mass, $F_g$, is vertically downward and is equal in magnitude to the space rate of change of the potential, i. e., $F_g = -\text{grad}\ \phi$.

The second term in equation (3), $p/\rho$, may also be interpreted as a potential, defined for every point throughout the region occupied by the liquid. This is the potential due to the internal stress of the material and is called the pressure potential. It has been designated by the letter $\pi$[8]. At any point in the liquid,

$$\pi = p/\rho \qquad (5)$$

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[7] Bernouilli's equation is valid for steady irrotational motion of a uniform frictionless fluid.

[8] The more general expression (*17, p, 149*) for the pressure potential at a point $B$ is, $\pi = \int_A^B dp/\rho$ where $A$ is the arbitrarily chosen point of zero pressure potential. This expression holds for both positive and negative pressures and is valid through varying densities. When $\rho$ is constant the above integral reduces to $p/\rho$ where $p$ is the difference in pressure between $A$ and $B$.

When dealing with the gravity potential, the work done in raising a unit mass against gravity may be

where $p$ is the value of the pressure at that point. In the case of water, $\rho$ is equal to unity, and hence for this liquid $\pi$ is numerically equal to the pressure. It is a matter of common observation that if a horizontal tube is filled with water and there is a difference in the pressure at the two ends, the water will flow from the high to the low pressure end. Let us consider a unit cube of liquid in such a tube in which there is a difference in pressure of 1 dyne per square centimeter per unit of length in the horizontal direction. When this condition exists the pressure force on one end of the cube will be 1 dyne greater than the pressure force on the other end and there will be a resultant force of 1 dyne per cubic centimeter, tending to move the water in the direction of the decrease in pressure. It should be noticed that under the conditions of this example the pressure potential has a gradient of one potential unit per centimeter in the direction of the increase in pressure. Hence, the property of the electrostatic potential set forth in equation (1), is also a property of the pressure potential, i. e., the field force, $F_p$, due to the pressure in the liquid is equal to the negative potential gradient or, $F_p = -\text{grad}\ \pi$.

In working with potential functions the potential gradients and potential differences are the significant quantities, and these are independent of the place chosen as the reference level or place of zero potential. That is, if a different reference level were chosen the potential would take on a new value for every point, but the size and *direction of the potential gradient* at any point or the difference in potential between any two points would remain unaltered. For the systems considered in this paper, and for soil-moisture work generally, it will be found convenient to choose the same reference level for both the gravitational and the pressure potential, i. e., the region of zero hydrostatic pressure or the free flat water surface.

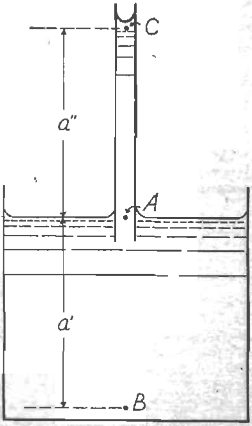

FIG. 1.—Capillary tube dipped into a free water surface

With the pressure at the free flat water surface chosen as the zero reference level for $\pi$, then the value of $\pi$ at all other places is simply equal to the difference in pressure between the flat water surface and the point in question. If at a given point the pressure is less than at the surface, then $\pi$ is negative, and vice versa.

Let us consider a system in which both the pressure and gravity force fields are acting. If a capillary tube is dipped into a free surface (fig. 1) the water will rise in the capillary tube and come to rest. When the water is at static equilibrium the forces on each little element of water must be balanced. Hence, there must be some force

acting in the liquid to neutralize the force of gravity. The forces that are acting may be derived by considering the potentials which are involved. Since the water is at rest, equation (3) must hold. Consider first the gravitational potential. For all points at the same level as $A$, which is at the level of the free flat water surface, $\phi=O$. At all other places in the liquid $\phi=gh$. That is, at $C$, $\phi=ga''$, and at $B$, $\phi=ga'$. The gravitational potential at this latter point is negative because $a'$ is negative. From the expression $\phi=gh$, it is easily seen that all points in the same horizontal plane have the same gravitational potential. The potential gradient is always perpendicular to the equipotential surface, and in this case is vertically upwards. This is the opposite direction to gravity which is the field force of this potential.

$F_g=-\text{grad } \phi=g=980$ dynes $=1$ gm. $=$ gravity force per unit of mass·

According to the convention here adopted, the pressure potential $\pi$ is also zero at all points at the same level as $A$, where the hydrostatic pressure is zero. At other levels $\pi=p/\rho$.

The expression for the hydrostatic pressure in a liquid is $p=-\rho gh$, where $\rho$, $g$, and $h$ have the same meanings as previously used. Substituting this value for $p$ in the expression above gives $\pi=-\frac{\rho gh}{\rho}=-gh$. Therefore, at the point $B$, $\pi=-ga'$. Because $a'$ is negative the value of $\pi$ at $B$ is positive and is numerically equal to the hydrostatic pressure in the liquid at that level. At the point $C$, $\pi=-ga''$. $\pi$ is negative at $C$ because $g$ and $a''$ are both positive quantities. The negative sign indicates that the water at the point $C$, just under the meniscus, has a negative pressure, or that it is under tension. Thus, the pressure and the pressure potential are positive at $B$, decrease to zero at $A$, and become more and more negative with increasing height in the capillary tube.

The equipotential surfaces of the pressure potential are horizontal because all points at the same level have the same hydrostatic pressure. However, the gradient of $\pi$ is vertically downward because that is the direction in which $\pi$ increases. The field force due to pressure difference is in the opposite direction to the gradient, and hence acts vertically upward. Pressure and gravity are the only force fields acting in a system such as Figure 1, so if the water is in static equilibrium the pressure and gravity forces on each little element of water must be balanced. There must be at every point a force due to a pressure gradient which is just equal and opposite to the force of gravity.

If at every point in the region just considered we add together the value of $\pi$ and $\phi$ we shall have a new point function which we shall call $\Phi$, the *total potential.*

$$\pi+\phi=\Phi \tag{6}$$

$\Phi$ has the same properties as the two potentials of which it is composed. Grad $\pi$ is a measure of the forces set up due to the internal stress of the water, grad $\phi$ is a measure of the force due to gravity, while grad $\Phi$ is a measure of the resultant of both of these forces acting on a unit of mass at any given point. Since the system we have just considered is at static equilibrium the resultant of all the forces

acting on each little particle of the liquid must be zero, and hence there must be no gradient of the total potential. This is the condition set forth by equation (3), and it is easily seen to be true, for

$$\pi + \phi = -gh + gh = \Phi = 0 \tag{7}$$

everywhere in the system. At the water surface $\pi = 0$, $\phi = 0$, and therefore $\Phi = 0$. Everywhere else $\pi$ is just the negative of $\phi$, so that they add up to zero. Thus the space occupied by the water in the system is an equipotential region for $\Phi$, and because of the reference level convention that has been adopted, $\Phi$ is everywhere equal to zero. When this condition obtains the gravity and pressure forces

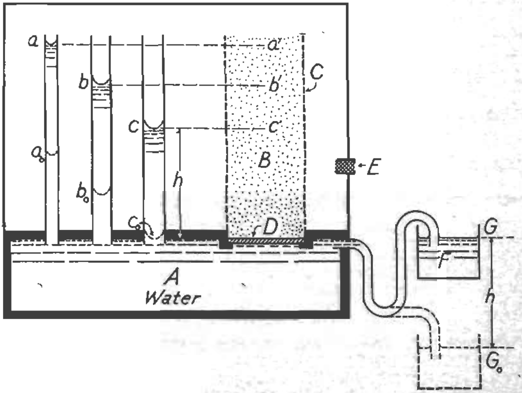


FIG. 2.—A system to aid in studying the moisture relations in a soil column. See text for complete explanation

are just balanced and, neglecting friction, a very slight impulse would be sufficient to move a little mass of water anywhere in the system.

As an example more closely related to the soils problem let us consider the forces and potentials in the system illustrated in Figure 2. A is a water tank fitted with capillary tubes as indicated. B is a column of soil supported by a cylindrical sieve, C, and closed at the bottom with a porous clay plate, D, readily permeable to water. The vertical tubes are inclosed in a case which is provided with a porous plug opening, E, to maintain atmospheric pressure within, but to prevent the loss of water vapor from the chamber. When the tank, A, is filled, and the water in the auxilary tank, F, is so adjusted that the free water surface is maintained at the level, G, then water will rise in the capillary tubes and soil column and will reach an equilibrium distribution, provided the temperature everywhere in the system is maintained uniform.

To simplify the problem, let us here assume that pure water and washed soil are used. When the system has come to equilibrium under isothermal conditions, let us say that the water has risen in the capillary tubes to the heights $a$, $b$, and $c$, respectively. These heights will be determined by the radii of the tubes and the surface tension of the water according to the formula $h=\frac{2T}{rg}$ where $g$ is the acceleration of gravity, $r$ is the radius of the tube, and $T$ is the surface tension of the water (c. g. s. units implied).

The configuration of the region occupied by the water in the soil is not definitely known, but it is probable that in moist soils the water forms a continuous and connected configuration which spreads out in thin films over the surface of the soil grains and collects into wedges where the grains are in contact or are very close together. It is the relation between the potentials and the forces in this water configuration that we are particularly interested in.

In Figure 2, all points in the liquid at the same level as G—the level of the free water surface—have $\pi=0$, $\phi=0$, and hence, $\Phi=0$. We shall consider the pressure and gravity force relations in the soil-water configuration quite analogous to those existing in a capillary tube. The forces and potentials may be analyzed by the same method that was used for the system shown in Figure 1, and at equilibrium—according to equation (3)—$\Phi$ must have the same value everywhere in the region occupied by the water.

It is well known that the vapor pressure of a liquid depends on the curvature of the liquid surface (*3*). When equilibrium exists in the system of Figure 2, the water surfaces in the soil at $a'$ must have the same curvature as the capillary meniscus at $a$, for if such were not the case there would be a difference in the vapor pressure at the two points. This would result in distillation and in the motion of water in a cycle, which, according to the second law of thermodynamics, is impossible under isothermal conditions.

As was shown above, $\pi$ has the same value for all points in the capillary tubes or soil column which are at the same height above the free water level, G. This means that the pressure in the liquid at all these points is the same. That this is the case may be indicated by the following different method of reasoning. When equilibrium obtains, all the liquid surfaces at the same height have the same vapor pressure and hence the curvature of the air-water surfaces in the soil at $a'$, $b'$, and $c'$ is the same as that at the corresponding heights, $a$, $b$, and $c$, in the capillaries. (Pure water and constant temperature are assumed.) The difference in pressure on two sides of a curved liquid surface is given by the well-known formula

$$p=T\,(1/r_1+1/r_2) \tag{8}$$

$T$ is the surface tension of the liquid in dynes per centimeter and $(1/r_1+1/r_2)$ is the expression for the total curvature of the surface.[9] The surface tension and curvature have the same values at both $a$ and $a'$, and since the pressure in the vapor at $a$ and $a'$ is prac-

[9] $r_1$ and $r_2$ are the radii of curvature of the two curves formed by the intersection of two planes (principal planes) at right angles to each other and passing perpendicularly through the water surface at the point where it is desired that the curvature be known.

tically equal to the pressure in the water at the flat surface (neglecting the pressure difference in the vapor between $a$ and D due to the weight of the column of gas between these two points), then the value of the pressure difference in the liquid between the points $a$ and D, and $a'$ and D, is given by equation (8) and is numerically equal to $\pi$. Hence, the value of $\pi$ when determined in this manner will be the same for all points at the same level because the surface tension and curvature are the same at all these points.

The above reasoning holds, of course, only for pure water in an isothermal equilibrium system. However, if we still retain the assumption that $\rho$ is equal to unity, then the value of $\pi$ in soil water is correctly given by equation (8), even if isothermal equilibrium conditions do not obtain.

CAPILLARY POTENTIAL

The preceding discussion of potentials was given primarily as a preparation for introducing and defining the capillary potential, which we shall designate by the letter $\psi$. The value of this function at a given point in moist soil was originally defined by Buckingham (*2*) as the work that would have to be done against the "capillary field force" in transferring a unit mass of water *from the soil to free water* at zero hydrostatic pressure. Subsequent writers (*4*, *8*), however, have defined this function as the work done against the capillary field force in moving unit mass of water *from the flat water surface to the point in question*. This definition gives $\psi$ the opposite algebraic sign to that used by Buckingham. This latter definition is more in accord with the way potentials are ordinarily defined and is the definition that will be used in this paper.

Just what is meant by "capillary field force" is rather obscure. If we interpret this expression, as Buckingham indicated, as simply the mechanical force involved in the attraction of moist soil for water, then we may consider it as the force set up in the soil water configuration due to pressure differences or due to a pressure gradient. When this is understood, it is easy to see that the capillary potential and the pressure potential are the same. That is,

$$\psi = \pi \tag{9}$$

No one questions the significance of the pressure potential when studying the flow of water through pipes or the motion of ground water where the soil is saturated, but in soil which is not saturated, the pressure in the water is negative, and for studying the flow of water under such conditions neither the pressure potential nor the capillary potential has been very much used.

That the pressure is negative makes little difference. The potential functions should be as useful in soil-moisture work as they have been in dealing with electricity or heat. Failure to use capillary potential when making a detailed study of the flow of water through soil is almost as inconsistent as not taking advantage of the well-known equation of Fourier [10] when studying the flow of heat at temperatures below zero, because the distinction between positive and negative pressures is almost as arbitrary as the distinction between positive and negative temperatures.

[10] Fourier's equation for the flow of heat will be discussed further on in the paper.

Because of its descriptive fitness, capillary potential will be used for regions such as moist soil where the hydrostatic pressure is negative; but it should be understood that the two terms, capillary potential and pressure potential, are interchangeable. The place of zero hydrostatic pressure has been chosen as the reference level. The capillary potential will therefore be negative in moist soil or wherever the hydrostatic pressure is negative.

### MEANS OF CONTROLLING CAPILLARY POTENTIAL

With the proper arrangement of porous clay apparatus the capillary potential in soil which is in contact with the porous surface may be accurately controlled. Let us refer again to Figure 2. When the water surface in the auxiliary reservoir is at the level G, the meniscus in the largest capillary tube, *c*, is at a height $h$ centimeters above G. This height corresponds to a capillary potential of $\psi = -gh = -980h$ dyne centimeters per gram. (This is equivalent to a tension of 980 $h$ dynes per square centimeter in the water at *c*.) Now if the reservoir, F, is lowered so that when the system again comes to equilibrium the new free water level is $h$ centimeters lower than before, then the meniscus in each capillary tube will be depressed by this amount. Under the new conditions the curvature of the water films in the soil on the porous plate is the same as that which previously obtained at the height $h$ centimeters above the plate, because this curvature is the same as the curvature of the water meniscus now at $C_0$. The value of $\psi$ in the soil on the plate is negative and is numerically equal to $g$ times the vertical distance down to the new free flat water surface. It is evident that with the initial conditions (free water level at G) the curvature and pressure relations obtaining at any point in the soil column would be unchanged, if, at some position lower in the soil column, a horizontal porous plate were interposed, the plate being mounted in such a way that its under side could be kept in contact with a column of water reaching down to the free water surface. When using the centimeter-gram-second units, the capillary potential in soil which is in equilibrium with water through a porous plate is numerically equal to the difference in pressure in the water under the plate and the atmospheric pressure. This pressure difference may be determined by means of a water or mercury manometer. With porous clay apparatus of sufficient strength and fineness of porosity, pressure differences as high as 1 atmosphere may be maintained in this manner.

In the system illustrated in Figure 2, the conditions of uniform temperature, pure water, and static equilibrium throughout the system were assumed. These conditions of course would be impossible to attain in any actual soils experiment. Nevertheless, the methods used in this example for deriving the capillary and gravitational field forces from their corresponding potentials may be quite generally applied.

When the soil moisture is not at static equilibrium with free water, then the relation $\psi = -gh$ no longer holds. For liquids of constant density $\psi$ is defined by equation (5), i. e.:

$$\psi = p/\rho \qquad (10)$$

For soil-moisture work generally we may assume $\rho$ equal to unity[11] because the errors involved in measuring $\psi$ will be greater than those introduced by this assumption. Equation (10) then becomes

$$\psi = p \tag{11}$$

where $p$ is simply the pressure difference between the reference level and the point in question (c. g. s. units implied).

### Apparatus for Measuring Capillary Potential

When the tension in the soil water is less than 1 atmosphere, the value of $\psi$ in a given soil may be accurately determined by a direct method. The apparatus shown in Figure 3, called a capillary potentiometer, has been used in this laboratory for various soil experiments. It consists of a porous cup, A, sealed onto a glass tube which is connected by heavy pressure tubing to a mercury manometer, B. The porous cup and the manometer are filled with water, a rubber stopper is inserted at C, and the cup is imbedded in soil. When water moves from the cup into the soil, the mercury rises in the manometer and the pressure within the cup is reduced. This process continues until the soil water and the cup water have the same pressure. The difference between this pressure and atmospheric pressure is numerically equal to the capillary potential of the soil and may easily be determined by properly reading the manometer.

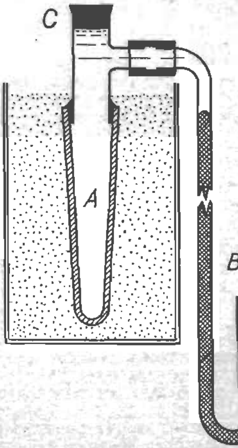

FIG. 3.—A capillary potentiometer. See text for complete explanation

When using equations (2) and (3) the pressure difference should be expressed in dynes per square centimeter and would correspond to a potential in dyne centimeters per gram (work per unit of mass). However, for practical purposes these units give large numbers with which to deal. The capillary potential may be conveniently expressed in terms of the length of the water column which the tension in the soil water would be able to support. If the length of the water column is given in centimeters, then the potential units would be gram centimeters per gram and would correspond numerically to the tension in the liquid expressed in grams per square centimeter.

[11] $\rho$ is sometimes used to represent the mass of water per unit aggregate volume of the soil (*5*, *6*, *8*), but in this paper $\rho$ is used only to represent the mass per unit volume of water or soil solution.

### Factors Determining the Capillary Potential

As was seen from considering Figure 2 and the definition of $\psi$, the *equilibrium value* of the capillary potential in a soil column at a given height above a free water level is a constant, independent of soil structure, temperature, or dissolved material in the soil solution. The percentage of moisture in the soil at this height, however, varies with all of these factors.

$\psi$ is a magnitude determined by the pressure in the water. Because of our choice of the pressure reference level, water is said to be under tension when its pressure is less than atmospheric pressure. (The pressure in water at a free flat water surface is the same as atmospheric pressure.) The difference in pressure between the water under the little curved surfaces of the soil solution and the atmosphere is given by the formula (8) $p = T\left(\frac{1}{r} + \frac{1}{r_2}\right)$. If we could measure the surface tension and surface curvature of soil water, then we would be able to calculate the value of $\psi$ at any point. This would be unnecessary for certain values because, as was seen earlier, the potential can be measured directly by means of the capillary potentiometer.

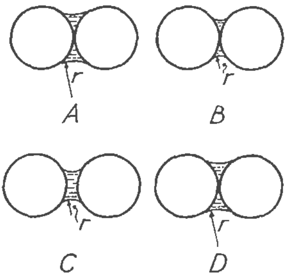


Fig. 4.—Water wedges between spherical soil particles. Decreasing the amount of water between articles (A) increases the curvature of the water surface (B); pressing the particles closer together (C) decreases the curvature (D)

Let us now see how the value of $\psi$ in a given *isolated* mass of moist soil is affected by the temperature, moisture content of the soil, dissolved material in the soil solution, size of soil particles, and state of packing. Any change which increases the surface tension or the curvature will decrease $\psi$, and vice versa.[12]

For a mass of soil with a certain state of packing and water content, decreasing the temperature or increasing the amount of dissolved salts in the soil solution will increase the surface tension and hence decrease $\psi$. The other factors—moisture content, size of soil particles, and state of packing—will affect the value of $\psi$ through their effect on the curvature. As is indicated in Figure 4, A and B, if the amount of water collected between two soil grains is decreased, there will be an increase in the curvature of the water surfaces, hence a decrease in $\psi$. That is, the drier the soil, the more negative the capillary potential will be. Also, if equal weights of a fine and a coarse soil have the same moisture percentage, the fine soil will have more surface and more contact points between soil particles. There will be less water collected at each of the contact points, and it would be expected that the fine soil will have a lower potential than the coarse soil even though their moisture percentages are the same.

[12] The magnitude of $\psi$ will be spoken of in the algebraic sense. That is, $-5$ is greater than $-10$, or, as a further example, $\psi$ *increases* if it changes successively from $-10$, $-5$, 0, 5, 10, and so on.

The compactness of the soil also influences $\psi$. Referring again to Figure 4, C and D, if two particles of soil are pushed closer together the curvature of the water surface will be decreased. If comparatively dry soil is sufficiently compressed, water will run out under the force of gravity. During this process of compressing the soil (until the water is just ready to flow out) the moisture percentage, expressed on the dry-weight basis, remains unchanged, but $\psi$ changes from a low negative value to zero.

For a magnitude that has as many influencing factors as $\psi$ it is desirable to hold all the factors constant except one and see how the magnitude varies when this one factor is changed. In studying the capillary potential the moisture percentage of the soil seems to be the factor best suited for this purpose. If the contact angle between

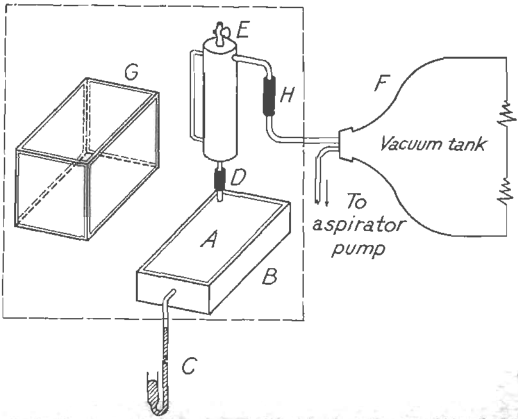


FIG. 5.—The arrangement of the apparatus for determining the capillary potential in soil. See text for complete explanation

water and the soil particles is zero, we should expect that for a given soil, having a certain temperature and state of packing, there would be a certain definite value of $\psi$ for each value of the moisture percentage. All the experimental data thus far collected seem to support this conclusion.

MOISTURE PERCENTAGE EXPERIMENTAL DATA.

As was pointed out earlier, the value of $\psi$ in soil which is in equilibrium with water through a porous plate is numerically equal to the difference in the pressure in the water under the plate and atmospheric pressure. By making use of this fact the apparatus shown in Figure 5 served to determine the moisture percentage-capillary potential curves for several types of soil. The porous plate, A, was specially made for the purpose, and is 9 inches long, 5 inches wide, and about one-fourth inch thick. It is mounted in the cast aluminum case, B,

and an air-tight seal is effected by means of plaster of Paris and a soft wax. The mercurial manometer is connected at C. A ⅜-inch copper tube is sealed in to the porous plate at D and a vacuum rubber connection made to the water reservoir, E. To put the apparatus in operation the manometer is supplied with mercury and the capillary cell and reservoir are filled with water. The corner of the plate at D is slightly raised so that any air which accumulates within the cell may pass upward through the water in the reservoir. By means of an aspirator pump the pressure in the vacuum tank, F, is reduced until the mercury stands at the desired level in the manometer. The soil for the experiment is then spread on the plate to the desired depth and covered with the glass cage, G. The soils used were air-dried and reduced to a fine powder by means of a small hand grinder.

Four of the complete units shown in Figure 5 were used. That part of the apparatus within the dotted line was mounted in an air thermostat, the air being well stirred by an electric fan. For the data here presented the temperature was maintained at 16.1° C. During the course of the experiments, continuous thermographic records were kept, and except for short intervals when samples were taken, the temperature fluctuations were less than one-tenth of a degree centigrade. The interior of the case was kept dark to avoid the temperature effects of light observed by Linford (*12*). When the apparatus was ready the plates were covered with a ½-inch layer of soil, the glass cover cages installed, and the thermostat closed. The dry soil absorbs water from the porous plate until the soil moisture is in pressure equilibrium with the water under the plate. Since the maximum distance the water moves through the soil is one-half inch, this equilibrium is rapidly approached. The carboy pressures were adjusted so that the mercury levels in the manometers remained constant from two to four days to permit the soils to reach equilibrium. At the end of this time 40 to 50 gm. soil samples were taken from the plates and the pressures set at some new values. The moisture determinations were expressed as percentage of water for dry weight of soil. The data for four different soils are given in Table 1 and Figure 6.

TABLE 1.—*The moisture percentage and capillary potential values of four soil samples*

[The moisture is expressed as percentage of water for dry weight of soil and the corresponding capillary potential is given in gram centimeters per gram]

| Bennet sand | | Greenville loam | | Trenton clay | | Preston clay | |
|---|---|---|---|---|---|---|---|
| Moisture | Potential | Moisture | Potential | Moisture | Potential | Moisture | Potential |
| 20.9 | 4 | 39.6 | 5 | 67.3 | 4 | 66.5 | 6 |
| 11.7 | 26 | 34.2 | 29 | 52.5 | 27 | 60.4 | 22 |
| 9.5 | 54 | 30.2 | 55 | 45.2 | 53 | 57.8 | 31 |
| 7.6 | 82 | 27.0 | 84 | 43.0 | 64 | 51.5 | 58 |
| 6.9 | 110 | 22.8 | 144 | 40.5 | 82 | 46.3 | 85 |
| 6.2 | 150 | 20.5 | 222 | 38.0 | 103 | 42.4 | 143 |
| 5.7 | 240 | 19.4 | 269 | 33.6 | 125 | 40.2 | 196 |
| 5.3 | 348 | 19.0 | 304 | 30.7 | 216 | 33.0 | 287 |
| 5.1 | 301 | 17.5 | 371 | 28.4 | 286 | 31.6 | 438 |
| 4.9 | 427 | 17.0 | 429 | 27.2 | 380 | 31.2 | 362 |
| 4.8 | 452 | 16.4 | 489 | 26.2 | 467 | 29.4 | 527 |
| 4.7 | 492 | 15.5 | 556 | 26.2 | 558 | 29.0 | 650 |
| 4.1 | 684 | 15.2 | 656 | 24.5 | 800 | 28.7 | 729 |
| 4.0 | 596 | 13.0 | 715 | 24.3 | 612 | 28.5 | 664 |
| 3.9 | 692 | 14.6 | 796 | 24.2 | 735 | 28.4 | 611 |
| 3.7 | 801 | ------- | ------- | 24.0 | 745 | 28.3 | 784 |
| ------- | ------- | ------- | ------- | 23.8 | 555 | 27.7 | 776 |

Since $\psi$ is negative, the fourth quadrant is used for plotting. The soils used were: A, a loose sandy loam; B, a clay loam; C, a heavy subsoil clay; D, a fine clay from Preston, Idaho. (The porous plates were made from Preston clay.) The potential units used in plotting are gram centimeters per gram, and correspond numerically to the length in centimeters of the water column which the tension in the water would be able to support.

If large soil tubes 26 feet high were filled with these soils at the temperature and state of packing here used, and with their lower ends dipped into free water were allowed sufficient time for the water to come to static equilibrium, then the distance above the flat water level would correspond numerically to the potentials, and

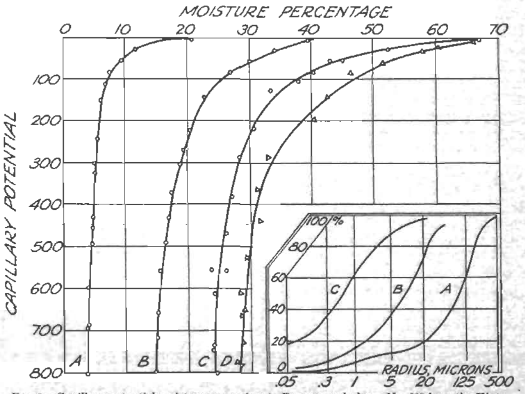


FIG. 6.—Capillary potential-moisture curves for: A, Bennet sandy loam No. 629 from the Uinta Basin; B, Greenville clay loam from the college farm; C, Trenton subsoil clay No. 1232; D, clay from Preston, Idaho. The inset shows the mechanical composition of soils A, B, and C, the ordinates showing the percentages of material of smaller radius than the corresponding abscissas

the moisture percentages at any height up to 800 centimeters (26 feet) for the different soils could be determined from the curve.

The mechanical analyses for soils A, B, and C, as given by Thomas (*19*), are shown in the inset, Figure 6. The effect of the size of the soil particles on the moisture content of soils at any fixed potential is very evident.

Because of the short distance the water has to move and the relative ease of duplicating the soil structure, the apparatus here described for determining the relation between $\psi$ and moisture percentage has some advantage over methods previously employed. The capillary conductivity seems to be less for clay than for sand, and the greater scattering of the experimental points from the smooth curves for the clays C and D indicates that for these soils two to four days was not sufficient time for the water to reach

equilibrium. Another source of error for this method lies in the fact that the mercury levels in the capillary cell manometers fluctuate with the atmospheric pressure. Continuous barographic records were kept to aid in compensating for barometric changes. For the low potential points the manometer (fig. 5, C) was replaced by a rubber tube reaching down to free water at the desired level. With this arrangement barometric fluctuations do not influence the value of $\psi$ in the porous plate.

## APPLICATION OF CAPILLARY POTENTIAL THEORY

### MOISTURE GRADIENT EXISTS

From the discussion given with Figure 2 it is clear that when moisture in a vertical soil column is at static equilibrium with a free water table, there must be in the water a gradient of the capillary potential having such direction and magnitude that the capillary or pressure forces just balance gravity. This means that the tension in the soil liquid must increase with the height above the water table. If the surface tension remains sensibly the same throughout the column, then, according to equation (8), the curvature of the air-liquid surfaces of the soil solution must increase with the height above the water table. As is indicated in Figure 4, this may be accomplished by having a looser state of packing, or by a decrease in the moisture content with increasing height above the water table. Experiments by King (*10*), Buckingham (*2*), Israelsen (*8*), and others indicate that the moisture gradient is necessary in order to make possible the proper capillary potential gradient for static equilibrium.

That this moisture gradient will exist under equilibrium conditions is still reluctantly accepted by some soils workers (*20*). The fact that this moisture gradient is not common in the field is easily explained. There is abundant evidence to show that the motion of water in dry soils is very slow. Under field conditions the seasonal and diurnal fluctuations of temperature, evaporation, precipitation, irrigation, and ground water, or drainage conditions make it unlikely that equilibrium is very closely approached in any actual case. Even if equilibrium were attained, the curves (fig. 6) indicate that for a deep-water table in the coarser soils the moisture gradient is so small that precise moisture-determination methods would be required for its detection. If static equilibrium were attained in a loam soil such as B, Figure 4, then a moisture gradient somewhat similar to that shown by the curve would be expected.

### SOILS NOT AT MOISTURE EQUILIBRIUM—CAPILLARY FLOW

Thus far we have considered only soil-water systems which were assumed to be at static equilibrium. The preponderance of evidence indicates that for actual cases in the field this condition is exceptional. Soil moisture is generally in motion. It is in the study of the dynamics of capillary flow that the potential theory is particularly useful. The reader is especially referred to the lucid nontechnical discussion given by Buckingham (*2*) on this phase of the subject; also to the more recent work of Gardner (*5, 6*) and Israelsen (*8*). This application of the potential theory is of prime importance because it offers a direct method for getting at the fundamental factors which determine

capillary flow. Because the above-cited literature is available this phase of the subject will be reviewed but briefly in this paper.

We have seen that grad $\Phi$, the gradient of the total potential, is a measure of the total "water-moving" force or the net resultant force (per unit of mass) which tends to produce motion of the soil water. Darcey's equation states that the velocity of the water is proportional to the force which is producing the motion, hence we may write,

$$v = -K \text{ grad } \Phi \tag{12}$$

where $v$ is the velocity and $K$ is the proportionality constant. Both the velocity and grad $\Phi$ are vector quantities because they have definite directions as well as magnitudes. Grad $\Phi$ is in the direction of the greatest rate of increase of potential. Since the water moves in the opposite direction the negative sign is used in the equation.

Equations similar to (12) are very useful in studying the flow of heat and electricity. Pointing out some of these similarities will aid in understanding equation (12) and help to attach a physical meaning to the constant $K$.

Fourier's law for the flow of heat is

$$q = -C \text{ grad } \theta \tag{13}$$

where $q$ is the velocity of flow, or the quantity of heat crossing unit area perpendicular to the flow in unit time. The temperature, represented by $\theta$, is a point function and may be spoken of as the thermal potential. Grad $\theta$ is the change in temperature per unit of distance in the direction of the greatest rate of increase in temperature. $C$, called the thermal conductivity, is a constant for a given kind of material. It is the amount of heat that would flow through a unit cube of the material in unit time if two opposite faces had a temperature difference of 1 degree. Qualitatively every one knows that a bucket of hot water will cool off faster in cold air than in warm air. This is because there is a greater temperature difference causing the heat to flow out through the walls of the bucket. Also the water would cool faster in a metal bucket than in a wooden one, because metal is a better heat "conductor." Equation (13) is a quantitative expression of these relations and simply states that the conductivity times the temperature gradient is equal to the heat velocity, or the quantity of heat transferred across unit area (perpendicular to the motion) per unit of time.

A similar expression has been found to hold for the electrical case. Ohm's law for steady electrical currents in metallic conductors may be written,

$$i = -C' \text{ grad } V \tag{14}$$

where $i$ is the current density, $C'$ the specific conductivity, and grad $V$ is the change in potential per unit distance.

From analogy with (13) and (14) we may call $K$ in (12) the specific capillary conductivity and define it as the amount of water which will flow in one second across a unit area in the soil, perpendicular to the direction of flow, when $\Phi$ changes at the rate of one unit per centimeter. However, the above analogy should not be pushed too far.

The thermal and electrical conductivities for a given piece of material are independent of the strength of the current and are in general only slightly dependent on the temperature and other outside influences, but the capillary conductivity $K$ will depend on the kind of soil, its moisture content, and state of packing.

It is true, of course, that before equation (12) can be usefully applied in actual problems this transmission constant will have to be studied for a large number of soils under different conditions, but this procedure seems to be our best chance for reducing the phenomena of capillary flow to a quantitative basis. This method has met with splendid success with heat and electricity and it should not be any more difficult to make reliable capillary potentiometers than it is to construct good thermometers or voltmeters.

For soil-moisture conditions where the tension in the liquid is not greater than 1 atmosphere, porous clay apparatus offers a convenient means for measuring and studying the capillary transmission constant. One experiment has been attempted in this laboratory with this end in view, but the experiment was unsuccessful because the apparatus was not of the proper design. However, with a short column of soil properly arranged between two capillary cells such as those shown in Figure 5, it should not be difficult to obtain a steady and measurable capillary flow from one cell to the other. The capillary potential gradient would be determined by the pressure difference in the water in the two cells and the moisture content of the soil could be determined from the capillary potential-moisture percentage curve for the soil.

The gradient of $\Phi$ may be computed from the relation

$$\text{grad}\,\psi + \text{grad}\,\phi = \text{grad}\,\Phi \tag{15}$$

Grad $\phi$ is a constant numerically equal to $g$. Potential gradients are vector quantities and must be added according to the parallelogram law which is used for the addition of forces. The resultant direction and magnitude of grad $\Phi$ determines the direction and velocity of the soil-water movement. When grad $\Phi$ and the velocity of flow, $v$, are known, the conductivity, $K$, may be evaluated by substituting in equation (12).

Three common cases of capillary water motion are: (*a*) Movement of precipitation or irrigation water downward through a comparatively dry soil, (*b*) motion of water upward from a saturated level or water table, and (*c*) motion of water in a horizontal direction. In case (*a*), grad $\phi$ and grad $\psi$ are such that both the gravity and capillary forces tend to move the water downward. This downward motion will continue (provided there is no surface evaporation) until the soil is drained dry or until the soil moisture comes to equilibrium with an impermeable layer or a saturated water table. In case (*b*), the gradient of the capillary potential $\psi$ has such direction and magnitude that there is a resultant upward "water-moving force." If there is no evaporation or transpirational loss of water from the surface the state of static equilibrium will ultimately be reached. However, when surface loss occurs, the capillary potential gradient is maintained and the upward flow continues. When the moisture content of soil is low the capillary conductivity is very small and

it requires large potential gradients (comparatively wet soil in contact with the dry) to produce an appreciable flow. Movement of water in a horizontal direction, case (*c*), is due entirely to a horizontal component of grad $\psi$. If undisturbed, the motion will continue until all points at the same level have the same potential.

### THE AVAILABILITY OF SOIL MOISTURE TO PLANTS

The problem of the availability of soil moisture to plants becomes very much simplified when considered in terms of the potentials. The term "availability" involves two notions, namely, (*a*) the ability of the plant root to absorb and use the water with which it is in contact, and (*b*) the readiness or velocity with which the soil water moves in to replace that which has been used by the plant.[13]

#### CASE (A)

For a plant which is growing in moist soil it is necessary for the root to absorb water from the little films and wedges among the soil particles. If the tension in the soil water is sufficiently high it is reasonable to suppose that the osmotic forces acting through the root-hair membranes may not be great enough to enable the plant to use even that soil water which is in contact with the root. The capillary potential is a measure of this tension in the soil water and, hence, should be a good index to the "security" with which the water is held by the soil. The term "security" as it is here used relates only to the pressure differences involved. Of course, it is possible for a plant to be in a wet soil and still be wilted and suffering from physiological drought if the salt content of the soil solution is sufficiently high. The effect of dissolved material on the availability of soil moisture which is in contact with the root could be expressed by adding to $\psi$ the value of the osmotic potential as used by Linford (*12*). For a more complete index to soil-moisture condition it would be possible to use thermodynamic potential or free energy (*11*).[14] However, the capillary potential as here defined will be found useful over a wide range of soil-moisture conditions.

#### CASE (B)

The other factor in the availability of soil, namely, the rate at which water flows in toward the root, is concisely expressed by equation (12). The rate of flow across unit area perpendicular to the direction of movement is simply the conductivity times the potential gradient. Small potentiometers may be inserted at different points around a root system and without disturbing the plant the soil-moisture conditions can be carefully followed. If the conductivity and capillary potential for the soil have been investigated,

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[13] The above discussion assumes the position of the root to be fixed. It is probable that the ability of the plant root to extend itself is an important factor in determining the "availability" of water in relatively dry soils.

[14] When there are abnormally large amounts of soluble material in the soil water, or for dryer soils, where the water is in such thin films that it ceases to have the properties of a liquid, then it would be advisable to use a function such as the free energy or thermodynamic potential. This function may be thought of as a sort of total potential which can be used in any kind of system and which would take account of the energy relations due to all of the factors such as pressure, gravity, osmosis, changes of state, chemical reactions, etc.

then the direction and velocity of the water movement can be approximated, if not accurately determined. Potentiometers, like the one illustrated in Figure 3, can be used to measure $\psi$ only when the tension in the liquid is between 0 and 1 atmosphere. It seems likely, though, that the optimum soil-moisture conditions for most of the agricultural plants lie well within this range.

The "old problem," as expressed by Livingston and Hawkins (*15*), that the commonly used methods of designating or describing soil moisture condition are "not ideal for ecological or agricultural inquires," is frequently expressed in the literature. Because of the difference in the security with which water is held by a fine and a coarse soil it is obvious that expressing the water content as a percentage of the dry weight of soil is not satisfactory. Expressing the moisture content of soil as a fraction of the moisture-holding capacity gives a better idea as to the availability of the moisture to the plant, but this method has the disadvantage that for a given soil the moisture-holding capacity will depend on such things as the temperature, the state of packing of the soil, and the length of time which is allowed for the soil to drain or to reach equilibrium. Also, when it is desired to maintain constant moisture conditions for potted plants over a period of time it is necessary to resort to the rather uncertain procedure of adding water to keep the pots up to the desired weight.

Because of the significance of the capillary potential concerning the "security" with which the water is held by the soil and also because of the ease with which the potential can be measured and controlled for experimental purposes, this function seems to have advantages over any of the magnitudes now used for designating or controlling soil-moisture condition as a factor in plant environment.

## MEASUREMENT OF $\psi$ IN DRY SOILS

Under ordinary conditions, such as in pipes, glass tubes, etc., it is difficult to subject water to very great tensile stress. If the lower end of a tall vertical cylinder with a carefully fitted piston were submerged in water and the air removed from beneath the piston we could, by raising the piston, make the water stand in the cylinder to a height of 28 to 32 feet, depending on the barometric pressure. If we attempt to increase this height by further raising the piston the water simply breaks into the vapor phase because the liquid will not stand any further decrease in pressure or increase in tension. There is evidence, though, that if proper conditions are obtained the tension may be increased for beyond this value. Some workers believe it is possible for water to support tensile stresses as large as 10,000 atmospheres. The conditions in a dry soil are such that the water is under extremely high tension. When the tension is greater than 1 atmosphere, then the ordinary potentiometers can not be used for measuring $\psi$.

Since the vapor pressure of the soil water depends on the surface curvature of the soil solution, the vapor pressure of the soil can be measured and the corresponding capillary potential can be calculated

if the vapor pressure of the soil solution at zero curvature is known.[15] Calculations based on vapor-pressure data and the wilting coefficient given by Thomas (*18*) indicate that wheat plants can grow and absorb soil moisture which is under tensions as high as 26.4 atmospheres before wilting occurs. This is the moisture condition that would have existed if the soil had been at equilibrium with a water table 896 feet lower.[16]

The measurement of $\psi$ in comparatively dry soils might also be accomplished with apparatus having membranes by means of which the tremendous forces of osmotic solutions could be utilized. Some experimental work has been done in this laboratory toward the perfection of osmotic apparatus similar in form to the cells in Figure 5, and in which a copper ferrocyanide membrane was supported in a thin clay plate. However, as yet, no satisfactory cells have been produced.

## POSSIBLE IMPROVEMENTS IN APPARATUS

There is need for improvement and perfection of apparatus for use in connection with capillary potential measurement and control. More rugged and accurate potentiometers would be desirable for the purposes of field work. Pressure gauges could be used instead of manometers. The potentiometer should be provided with a sensitive means of detecting any motion of water from porous cup to the soil and should be arranged so that the cup water pressure can be reduced by hand until the outward flow ceases. Also, for certain kinds of work, the porous clay surface could be mounted as a section in the side of a metal pipe so that the instrument could be inserted some distance in soil without seriously disturbing the plant roots or soil structure. There is need for a recording potentiometer which can make continuous records. Capillary potential records taken over a period of years would furnish interesting information about the seasonal and yearly variation in the moisture condition of lower soil layers.

There is need also for improvement and commercial development of porous clay soil pots which will give satisfactory soil-moisture control for plant experimental work and possibly even for general use. Figure 7 shows a design that has been made up in this laboratory. A is a porous clay cup, shaped like an ordinary flower pot. It is

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[15] For a system such as that shown in Figure 2 it is evident that at each height above the water table there is a definite value for the vapor pressure as well as for the capillary potential. If there were a uniform concentration of soil salts dissolved in the water throughout the system, the vapor pressure everywhere would be reduced but the capillary potential gradient in the soil water and the pressure gradient in the column of vapor would still remain. In a column of water vapor the pressure, $p$, at any point, is given by the exponential $p = p_o\, e^{-\left(\frac{\rho_{vo} g h}{p_o}\right)}$, where $h$ is the distance of the point above the level where the vapor pressure and density are, respectively, $p_o$ and $\rho_{vo}$. If the vapor pressure of the water-saturated soil (zero hydrostatic pressure in the soil solution) is known, then the capillary potential in the soil at any other moisture content may be calculated from the vapor pressure of the soil by using the above formula.

Thomas found that wheat plants wilted when the vapor pressure, $p$, in Greenville soil was 2.330 cm. of mercury. This is 0.046 cm. less than the vapor pressure of the saturated soil at the same temperature. Thus, taking $p_o$ as 2.376 cm. of mercury and $\rho_{vo}$ as $23.11 \times 10^{-6}$ gm. per c. c., we can calculate $h$ from the above formula. Solving for $h$, we have

$$h = -\frac{p_o}{\rho_{vo} g} \ln \frac{p}{p_o} = \frac{2.376 \times 13.6 \times 980 \times 2.3 \times .0085}{23.11 \times 10^{-6} \times 980} = 27{,}336 \text{ cm}$$

This is numerically equal to the capillary potential (expressed in gram centimeters per gram) because the soil would have to be at this height in a soil column to be at equilibrium with the free flat surface of the soil solution.

[16] To avoid misunderstanding, it should be emphasized that even though wheat plants may be able to use soil water under tensions as high as 26.4 atmospheres, it is quite certain that water from an 896-foot water table would be "unavailable" for plant use because the rate of water movement would be too slow to supply the needs of the plant.

sealed into the can, B, by means of plaster of Paris and soft wax. A tube is fitted into the can at C and is connected to a pipe that reaches down to a free water surface. When the can and tube are filled with water and a stopper is inserted at D the capillary potential of soil in the pot will be determined by the height, *h*. This is essentially the same principle as that used by Livingston for his auto-irrigators (*14*). The type of apparatus here described has the advantage that the porous water-supplying surface is relatively larger and leaves the inside of the pot free to be occupied by the plant roots and soil. The porous clay material described in this paper was molded and fired in the laboratory. It is likely that with improved methods it would be possible to make the capillary cell unit A and B in Figure 7 out of one piece of fired clay, thus eliminating the sealed joint.

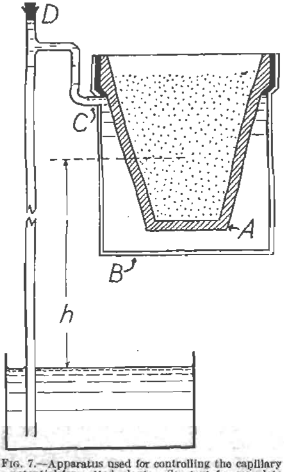


FIG. 7.—Apparatus used for controlling the capillary potential for potted plants. See text for complete explanation

There is need for the perfection of osmotic cells or other forms of apparatus for the measurement of $\psi$ in dry soil. It is possible to extend considerably the range of usefulness of the apparatus shown in Figure 5. If the soil on the plate were covered with an air-tight case so that by supplying air pressure in this soil chamber the pressure differences between the air in the soil and the soil solution could be greatly increased. The value of $\psi$ would be correspondingly decreased and determinations could be made at varying pressures.

## FURTHER EXPERIMENTAL DATA NEEDED

The capillary potential has as yet been only slightly used or applied in experimental work.

The following are some promising fields for experimentation that should yield valuable information: (1) Detailed experimental study of the capillary transmission constant for different soils with various states of packing and moisture content; (2) more complete study of the relation existing between capillary potential and soil-moisture content, mechanical composition, state of packing, temperature, and soluble salts; (3) study of optimum growth and germination potentials for different plants and experimentally determining whether or not $\psi$ is a more significant quantity than those now used for designating and describing soil-moisture condition as a factor in plant environment.

## SUMMARY

Studies on the movement of soil moisture and its availability to plants have been largely experimental and there is need of a comprehensive, guiding theory. The energy potentials and dynamical

methods which have been found so useful in studying electricity and heat may be equally well employed in soil-moisture investigations.

A discussion is given on the nature and use of potential functions, and the electrostatic, gravitational, pressure, capillary, and total potentials are defined.

It is shown that, when the proper units are used, the value of the capillary potential in soil which is in moisture equilibrium with water through a porous clay wall is numerically equal to the difference in pressure in the water and atmospheric pressure. The capillary potential is therefore a measure of the pressure in the soil solution.

The factors determining the capillary potential in a moist soil are discussed and experimental data are given which show the relation between this function and the percentage of moisture for four different soils.

The flow of moisture through soil can be expressed as simply the capillary conductivity times the potential gradient, i. e., $v = -K$ grad $\Phi$. (This is analogous to Ohm's law for electricity and Fourier's law for heat.)

Application of the potential theory to soil-moisture movement is made for the following cases: (1) Flow of moisture downward through soil after rainfall or irrigation, (2) flow of moisture upward from a saturated water table, and (3) movement of moisture in a horizontal direction.

The availability of soil water to plants involves two factors, viz, the "security" with which the water is held by the soil and the readiness with which moisture flows in to replace that which has been used by the plant. The capillary potential is a direct measure of this "security" factor. The rate of moisture flow toward the roots is quantitatively expressed in terms of the transmission constant and potential gradient by the above equation.

A new form of porous clay apparatus is described which can be used in controlling soil water for potted plants.

The capillary potential offers a means of quantitatively expressing soil-moisture phenomena and has advantages over the commonly used methods of designating soil-moisture condition as a factor in plant environment.

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# A STUDY OF THE EFFECT OF SURGICAL SHOCK ON INSECTS [1]

By William Robinson [2]

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## SURGICAL SHOCK IN MAN AND HIGHER ANIMALS

There is a form of shock in man that sometimes follows immediately after a wound is received. This form, called primary shock by Cowell,[3] resembles fainting and is caused by nervousness. It is not the direct result of the injury itself and usually lasts but a short time.

Surgical or traumatic shock is more deep seated and results from injury to the tissues. The injured individual grows pale, his skin becomes cold and often wet with perspiration, his pulse is rapid but very feeble, his breathing shallow, and his blood pressure low. These symptoms arise more slowly and last longer than in primary shock. They follow extensive burns, injury to the intestines, muscles, bones, testes, or other tissues. They also follow prolonged etherization.

The symptoms are produced, it is suggested, by the secretion into the blood stream of substances like histamine at the time of injury. Dilation of the capillaries follows and a flow of plasma takes place from the blood through the walls of the capillaries to the tissue spaces. This decrease in blood volume results in reduced blood pressure and increased heartbeat, accompanied by a reduction in the vital functions.

## A POSSIBLE COUNTERPART IN INSECTS TO SURGICAL SHOCK *IN HIGHER ANIMALS*

In a series of experiments conducted at this laboratory there has been found in insects a phenomenon which possibly may be interpreted as associated with traumatic shock. One of the effects is evident immediately after injury is received, but obviously the general symptoms must differ from those produced by shock in mammals.

The practical point of interest in shock of insects is, of course, the possibility that it may affect the insect's functions and cause distortion of physiological measurements, for severe injury to insects does result from some physiological tests. A knowledge of, say, the hydrogen-ion concentration of the blood of insects under various conditions is certainly of value, but in making the determinations it is necessary to puncture the insect and to express some of its lymph, and it may otherwise be mutilated. Moreover, in the determination of internal temperature the insect is pierced with the thermocouple point, for

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[2] Acknowledgments are due to Dr. R. A. Gortner, chief of the division of biochemistry, University of Minnesota, for the interpretation herein given of the results that follow the piercing of insects; and also to Dr. F. H. Scott, professor of physiology, University of Minnesota, who supplied the writer with information regarding surgical shock to man.

[3] Cowell, E. M. THE INITIATION OF WOUND SHOCK. [Gt. Brit.] Med. Research Council, Spec. Rpt. Ser. 25: [99]-108, illus. [1919.]

rectal readings are of doubtful accuracy in entomology, while there is always the danger of puncturing the wall of the rectum and causing local shock. In these and other instances the tissues are injured, and what appears to be traumatic shock is produced.

## EXPERIMENTAL DATA ON SHOCK OF INSECTS

Several species of insects, especially the pupae of the Polyphemus moth (*Telea polyphemus* Cram.), were used in the tests. Shock was administered by piercing some individuals with a needle. The body contents of others were expressed. All the tests produced an effect of such a nature that a marked disturbance of some kind was indicated. An immediate change occurred in the water relations of the tissues, due to the release of a large percentage of the water held by the cell colloids, as shown in Table 1. The technic used in making determinations of "bound" water has already been described by the writer [4] and will not be repeated here.

TABLE 1.—*Effect of shock on the quantity of bound water present in pupae of Telea polyphemus*

| | Percentage of bound water in— | | |
|---|---|---|---|
| | Normal individuals | Pierced individuals | Liquid expressed from body contents |
| | 27.5 | 19.1 | 9.6 |
| | 30.5 | 20.4 | 11.2 |
| | 21.3 | 17.4 | 5.3 |
| | 22.1 | 21.2 | 8.8 |
| | 20.8 | 17.6 | 7.6 |
| | 22.3 | 16.1 | 5.2 |
| Average | 24.1 | 18.6 | 7.9 |

In normal individuals an average of 24.1 per cent of the total water, as shown in Table 1, was in the bound condition. Piercing the tissues of others caused an immediate drop to 18.6 per cent, or a decrease of about 23 per cent of bound water. Expressing the body contents of other individuals caused a drop to 7.9 per cent, or the release of a still greater proportion, namely, of 67 per cent. The pupae used in these tests weighed on an average 4 gm. each, and of this weight about 71 per cent was total water. It can thus be seen that a relatively large change in the water relations takes place when shock occurs.

Fortunately, it has been possible to confirm these determinations by other data. The liberation of a large percentage of water at the time of shock would be expected to dilute the lymph and consequently to raise its freezing point. Therefore, a series of experiments was conducted to find the freezing point of lymph from normal and pierced individuals and also that of expressed lymph. The results are given in Table 2, where a rise in the freezing point is shown from −6.9° C. in normal individuals to as high as −2.1° in expressed lymph.

[4] ROBINSON, W. RELATION OF HYDROPHILIC COLLOIDS TO WINTER HARDINESS OF INSECTS. Colloid Symposium Monograph 5: 199-218, illus. New York, The Chemical Catalog Company, Inc. 1928.

TABLE 2.—*Effect of shock on the undercooling and freezing points of Telea polyphemus*

[Temperatures given in degrees centigrade]

| Insects in normal condition | | Insects pierced with needle | | Insects pierced with thermojunction, which remained in body during determination | | Expressed tissues and lymph | |
|---|---|---|---|---|---|---|---|
| Undercooling point | Freezing point | Under-cooling point | Freezing point | Under-cooling point | Freezing point | Under-cooling point | Freezing point |
| −15.2 | −6.8 | −6.7 | −3.8 | −7.3 | −2.7 | −5.8 | −2.0 |
| −15.2 | −7.5 | −5.2 | −3.7 | −6.8 | −2.6 | −5.1 | −2.2 |
| −15.4 | −6.2 | −7.5 | −3.9 | −5.6 | −2.7 | −4.7 | −2.3 |
| −15.6 | −7.0 | −7.6 | −3.9 | −6.3 | −2.3 | −4.8 | −2.0 |
| −15.2 | −7.0 | −6.5 | −3.9 | −6.8 | −2.6 | −4.8 | −2.1 |
| −15.4 | −6.8 | −7.1 | −3.7 | −6.2 | −2.5 | −5.4 | −2.1 |
| Average...... −15.3 | −6.9 | −6.8 | −3.8 | −6.5 | −2.6 | −5.1 | −2.1 |

The direct correlation which is thus established between percentage of bound water and freezing-point depression is shown in Figure 1. A theory to account for the unusual rise in the undercooling point at the time of piercing is mentioned in the paper that immediately

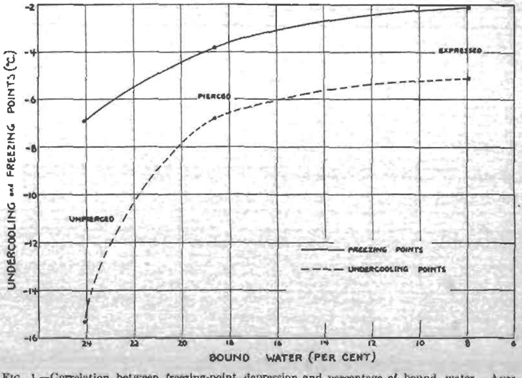


FIG. 1.—Correlation between freezing-point depression and percentage of bound water. Average of six tests

follows the present one. In the same article a description is given of a method of taking freezing-point readings without piercing.

The rapidity with which shock occurs after insects are pierced is shown in Figure 2 for pupae of *Telea polyphemus*. The broken line represents the descending body temperature of a number of unpierced individuals as the cabinet temperature fell slowly during 10 days. At practically any time during the descent the effect of shock

could be readily demonstrated. Piercing with the thermocouple caused an instantaneous rise in every case to the abnormal freezing point between −2.0° and −3.2° C. The difference between the normal and abnormal freezing points is further exemplified in this figure, for the unshocked pupae which were allowed to reach their normal undercooling point froze between −6.7° and −7.2°.

The rise in freezing point of over 4 degrees at the time of shock represents a large dilution of lymph and a great fall in osmotic pressure. It is difficult to account for this solely on the basis of liberation of bound water as determined. It may be that, due to shock, dissolved substances are removed from solution by adsorption.

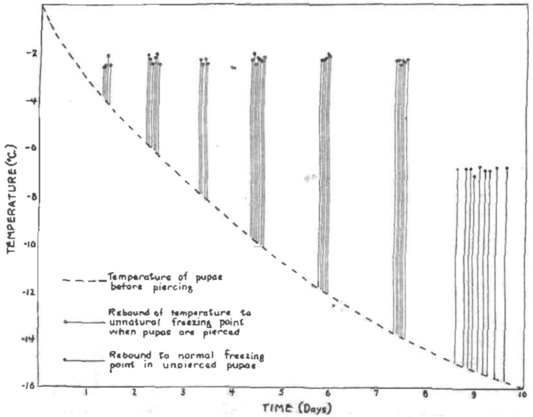


FIG. 2.—Curves showing rebound to abnormal freezing point at time of piercing and also the natural freezing point of normal specimens of *Telea polyphemus*

## A DISCREPANCY IN LOW-TEMPERATURE STUDIES EXPLAINED ON THE BASIS OF SHOCK

Normal insects when placed in a low-temperature cabinet have frequently been taken considerably below the expected undercooling point without becoming frozen. Carter [5] (1925) was probably the first to point out this discrepancy, and he suggested that the higher freezing point of pierced individuals was due to injury to the tissues.

Insects evidently possess greater resistance to low temperatures than has been apparent from freezing-point determinations. There are indications of a freezing zone for the different species which exists several degrees below the expected temperatures. A series of experiments was conducted to discover the temperature difference between

[5] CARTER W. THE EFFECT OF LOW TEMPERATURES ON BRUCHUS OBTECTUS SAY, AN INSECT AFFECTING SEED. Jour. Agr. Research 31: 165–182, illus. 1925.

the normal freezing zone and the abnormal freezing points as obtained by piercing. The procedure was as follows: A large number of normal insects of different species were placed in low-temperature cabinets and their temperature was allowed to drop slowly until the predetermined or abnormal undercooling point was reached. From there downward the specimens were cooled much more slowly—about 1.5° per day. Each day several individuals were examined for the appearance of ice crystals and then discarded. It was found that every species studied could be taken below the predetermined undercooling point before crystallization began.

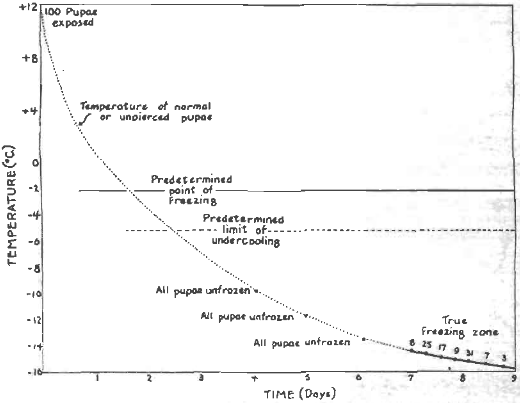


FIG. 3.—Curve showing the existence of a true freezing zone below the limit of undercooling as determined by piercing specimens of *Telea polyphemus*

The results secured for *Telea polyphemus*, which are typical of those obtained for the other species, are shown in Figure 3. One hundred normal pupae were used, and under a falling temperature they passed the abnormal undercooling point of −5.2° C. in two and a half days. The species is soft, and so freezing could be detected without dissection. The pupae were all lowered to −14.4° before freezing began, and some individuals resisted freezing down to −15.7°. This indicated a normal freezing zone between −14.4° and −15.7° for that species. Table 3 gives the results obtained for the other species in the series. In every case the normal freezing zone is several degrees below the undercooling point, and in some instances it is almost incredibly low.

**TABLE 3.**—*Comparison of predetermined freezing and undercooling points with normal freezing zone for all species tested*

| Species tested | Average predetermined freezing point (°C.) | Average predetermined undercooling point (°C.) | Normal freezing zone (°C.) |
|---|---|---|---|
| Full-grown wireworms (*Phyllophaga* spp.) | −1.6 | −3.8 | −12.1 to −15.2 |
| Colorado potato beetle (*Leptinotarsa decemlineata*) | −2.3 | −4.6 | −8.4 to −10.1 |
| Pupae of Polyphemus moth (*Telea polyphemus*) | −2.5 | −5.2 | −14.4 to −15.7 |
| Larvae of the willow sawfly (*Cimbex americana*) | −1.4 | −3.6 | −4.2 to −6.3 |
| Pupae of the dill worm | −2.8 | −4.2 | −8.8 to −10.3 |
| Pupae of the mourning-cloak butterfly (*Aglais antiopa*) | −2.2 | −3.7 | −7.1 to −9.9 |
| Adults of the granary weevil (*Sitophilus granarius*) | −4.6 | −8.3 | −18.0 to −22.1 |
| Black cabinet beetle (*Attagenus piceus*) | −3.2 | −7.8 | −15.5 to −18.6 |

## DESIRABILITY OF USING NORMAL MATERIAL FOR PHYSIOLOGICAL TESTS

Just as piercing or mutilation obscures the true freezing point of insects, so it is possible that other tests may likewise give incorrect values. In studying the reactions of a species to the various stimuli of its environment, it is the living normal organism that should be considered. The act of taking a physiological measurement may cause disturbances sufficient to alter the true condition. The question may therefore be asked whether it is justifiable to attach much significance to values thus obtained and to interpret responses on the basis of these values.

## SUMMARY

When insects are pierced, cut, or injured an effect is produced upon them that may be analogous to surgical shock in higher animals. This is most evident in the rapid change that takes place in the water relations. Since in some physiological determinations injury to the tissues is unavoidable, the data thus obtained may not accurately represent the condition in normal individuals.

# DETERMINATION OF THE NATURAL UNDERCOOLING AND FREEZING POINTS IN INSECTS[1]

By William Robinson

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## THE VALUE OF UNDERCOOLING AND FREEZING POINT DETERMINATIONS IN INSECT PHYSIOLOGY STUDIES

Although some species of hardy insects emerge normally in the spring after being frozen solid during the winter, the greater number studied at this laboratory have been found to perish if even partially frozen. There is, however, a marked difference in the susceptibility of different species to injury by ice formation within the tissues, and consequently freezing-point determinations are valuable in low-temperature studies.

Associated with the phenomenon of freezing is that temperature still lower in the scale, called the undercooling point, at which crystallization begins. With unpierced insects this has been found almost invariably to be several degrees below the freezing point. Since crystallization does not occur until the point of undercooling is reached, there is still a margin of safety for the organism; for if the temperature should cease to fall before that critical point is reached, the insect may escape freezing and death although it may have been cooled below its freezing point. In such a case it may survive if the exposure is not unduly prolonged.

The point of undercooling thus appears to be an important temperature also, since it probably represents the absolute minimum temperature for those species that are able to endure dormancy but can not survive freezing. This applies to comparatively short exposures only, for a low temperature may or may not be fatal according to the length of the exposure.

## HOW THE DETERMINATIONS ARE MADE

The undercooling and freezing points of insects are well-marked temperatures and can readily be determined. The procedure is essentially the same as that used in physics and chemistry. The material is cooled to the point where the temperature abruptly ceases to fall and begins to rise. This is the undercooling point. The burst of heat during the formation of ice crystals will raise the temperature of the material to its freezing point, and it will then remain constant for a length of time depending upon the mass used or the size of the specimen.

An insect the size of, say, a Colorado potato beetle, when placed in a cabinet at about −20° C., would undergo in a few minutes an internal temperature change approximately as shown by the heavy full line in Figure 1. With the aid of a thermocouple and a potentiometer outfit any point on this line can be determined.

[1] Received for publication Aug. 10, 1928; issued January, 1929. Published with the approval of the director as paper No. 796 of the Journal Series of the Minnesota Agricultural Experiment Station.

THE FREEZING POINT OF INSECTS

From the time the specimen is placed in the cabinet until it finally reaches the cabinet temperature it continues to radiate heat from its surface, and the warmer it is the greater, obviously, will be the amount of heat given off. Therefore at the time of rebound the heat radiation is increased, but the consequent loss of heat is not sufficient to prevent its temperature from reaching the freezing point. The fact that the temperature remains constant at the freezing point for some time after the rebound, as shown in Figure 1, indicates that an equilibrium has been reached between the heat lost by radiation and that gained by crystallization. Any excess of heat generated at the time of the rebound would not be lost by radiation but would be used up in melting ice crystals already formed. A failure of the rebound to reach

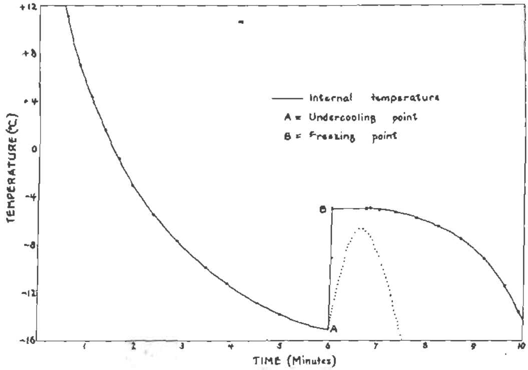


FIG. 1.—Internal temperature change of an insect the size of a Colorado potato beetle when placed in a cabinet at 20° C.

the freezing point would probably take the form shown by the faint dotted line in Figure 1, where the temperature would rise slowly and fall again without a pause. This, however, is a hypothetical case, for the writer has never observed it to occur even with very small insects, such as granary weevils, in which the proportion of surface to mass is large. A period of constancy at B has always been apparent.

## FACTORS AFFECTING THE RELIABILITY OF THE PIERCING METHOD

The most convenient method of making a determination is to impale the specimen upon the point of a thermocouple, and thus get the internal temperature reading direct. Unfortunately, however, piercing the tissues with the instrument has a physiological effect upon the organism which changes the position of the points to be determined. This effect is described by the writer in the article

that immediately precedes the present one. There it is shown that when an insect is pierced a shock is produced within the organism which is accompanied by a flooding of the tissues with free water, due probably to the release of bound water held by the cell colloids. As a result, the lymph becomes diluted and the freezing point is raised.

The position of the undercooling point is still more markedly disturbed by piercing, as is shown in Figure 1 of that article. The large elevation of the undercooling point of pierced individuals is probably due to the injection of crystal nuclei at the time of piercing. The phenomenon of freezing, being a crystal-forming process, is hastened by the addition of minute particles of material, many of which adhere to the needle or thermocouple point. It will be observed in the figure just mentioned (p. 745) that although the freezing point of *Telea polyphemus* was raised 3.1° at the time of piercing, the undercooling point was raised 8.5°.

For two reasons, therefore, the piercing method, although very convenient and rapid, appears to give inaccurate results; first, because of shock, and, second, because of injection of crystal nuclei.

## DETERMINATION OF INTERNAL TEMPERATURE WITHOUT PIERCING

When an insect is taken from a warm room and placed in a low-temperature cabinet standing at about −20° C., a sharp gradient of temperature is set up between the inner tissues of the insect and its surface, due to the loss of heat outward. The larger the insect the greater will be the gradient. If the temperature of the cabinet is constant the internal and surface temperatures of the insect will bear a definite relationship to each other, and if one is known the other can be estimated.

A thermojunction placed firmly against the surface of the insect will record a temperature lower than that of the surface, because the thermojunction is affected also by the temperature of the cabinet. The reading thus obtained is therefore a resultant of the two temperatures; but if the cabinet is held constant it is possible to employ the contact method to obtain the internal temperature record of the insect.

## A THERMOCOUPLE FOR CONTACT DETERMINATIONS

For contact readings a slight modification of one of the junctions of the thermocouple is required. The electromotive force of the thermocouple is set up at the point where the two dissimilar metals come together, and not at the tip. Therefore it is this point of union that must always be in actual contact with the material when a determination is made. Especial emphasis must be placed upon this fact for contact determinations; otherwise inaccuracies will occur and the rebound at the time of crystallization will be obscured. Moreover, the junction should be pressed firmly against the body of the insect, but not enough to distort the shape of soft forms.

A thermojunction with holder as shown in Figure 2 has been found satisfactory. The holder consists of a piece of glass or metal tubing, A, through which the thermocouple wires are run, and which

is then plugged at each end with a tightly fitting cork. The wires are run purposely between the cork and the tube, as shown in the end view of A, rather than through the cork. The thermojunction is then bent at right angles to lie against the face of the cork plug, so that the actual junction of the wires will come about the middle of the plug.

A simple device to hold the insect against the junction may be made as illustrated in Figure 2, B. It consists of a cork bored so that it will slide firmly up the tube, and to this cork a piece of tape of sufficient length is fastened with an adhesive band, such as zinc-oxide tape. The holder is then ready for use. When a determination is to be made the insect is placed in the loop of the tape and the tube is pressed down through the cork until the thermojunction comes in contact with the insect.

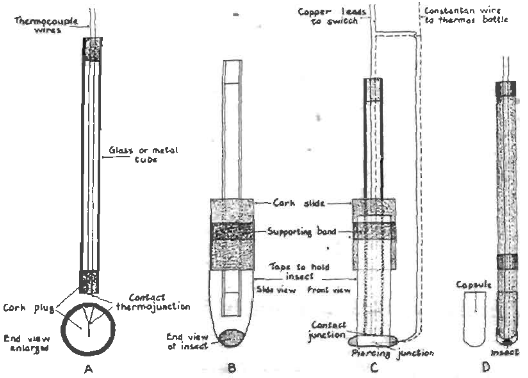


FIG. 2.—A thermojunction with insect holder for use in making contact temperature determinations. See text for detailed description

For small insects a still simpler device may be used. (Fig. 2, D.) It is made of a piece of wood rounded at one end and having a groove along two sides. The rounded end is made to fit firmly into a gelatin capsule. Capsules of this type may be readily obtained in several sizes. The thermocouple wires are run down the grooves and the junction is set at the rounded end. The insect is dropped into the capsule and the holder is pressed down until the thermocouple comes in contact with the insect.

## THE CORRELATION CHART

With the contact thermocouple ready for use, it remains to determine the relation between the surface temperature as recorded by contact and the actual internal temperature of the insect. This can be done by the use of a correlation chart, as shown in Figure 3. By

means of a thermocouple with combined contact and piercing junctions (fig. 2, C) both temperatures are taken close together at short intervals of time. When readings have been obtained thus for several individuals they are next plotted, as illustrated by the light dotted lines in Figure 3, the heavy full line being their average.

It is understood that the insects used in making the chart always give an inaccurate freezing point when pierced, but the actual freezing point of these individuals is of no value, since it is only the correlation between the internal and surface temperatures that is being sought. In fact, piercing in these instances has an advantage in giving a higher

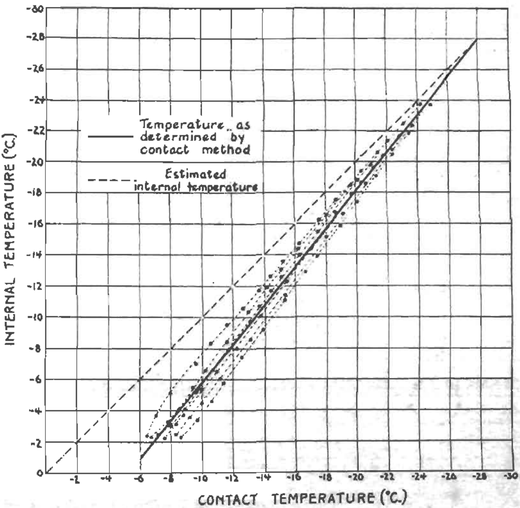


FIG. 3.—A correlation chart to be used in determining the actual internal temperature of an insect from its surface temperature as recorded by contact

initial freezing point and a longer range than could otherwise be obtained.

The two copper leads (fig. 2, C) from the combined contact and piercing thermocouple are connected to a rotary or a 2-way switch to permit one junction to be disconnected and the other to be connected to the galvanometer at one movement. This arrangement allows readings of the internal and contact temperatures to be taken very close together, which is important. The temperature of the freezing cabinet must be held constant; and the thermojunction with holder must be placed in the cabinet and allowed to come into equi-

librium with it before any readings are taken, as a varying temperature of the thermojunction holder must be avoided.

When a determination is to be made, the thermojunction holder is taken out of the cabinet, the insect is placed lengthwise in the loop, and the junction is pressed fairly firmly against the insect. The piercing junction is then inserted in the body and the holder and insect are placed in the cabinet. This should all be done as quickly as possible to prevent the temperature of the junction holder from being unduly raised. The temperature gradient between the interior and the surface is too sharp at this time to be measured accurately; that is, the two temperatures will change so quickly that if they are taken now they will not represent their correct relationship to each other. Apparently the most practicable time to begin is when the rebound to the freezing point has occurred. From there downward several readings for each insect should be taken. When readings for several individuals have thus been obtained and the data plotted to show internal temperatures on one axis and contact readings on the other, a correlation curve for the mean can be secured.

The first three or four determinations for any individual will not always follow a straight line, as seen in the faint dotted lines in Figure 3. This is probably because at the higher temperatures the insect is still soft and permits a movement of the piercing junction within its body across the sharp gradient. After freezing occurs the junction remains stationary and the line flattens out.

The chart will possibly hold only for the species for which it was made, others probably being necessary for other species. The diameter of the insect and the hardness of the surface are important limiting factors. For very small species it is difficult to make a chart. However, it has been observed that the smaller the species the less is the difference between its contact and internal temperatures. Decrease in size means a corresponding reduction in temperature gradient. The writer has found that in the case of rice weevils, which are very small hard beetles, the undercooling point, as indicated by contact, appears to be very close to the undercooling point in nature, for the weevils will not begin to freeze until approximately that temperature is reached.

It will be noticed in Figure 3 that as the exposed insects become colder their gradient decreases. The heavy full line approaches the heavy broken one, and the two meet at the temperature of the cabinet—which is exactly what would be expected. It follows, therefore, that the lower the contact reading the nearer will it be to the true internal temperature.

## MAKING CONTACT DETERMINATIONS

When the correlation chart is ready it will be possible to approximate the natural undercooling and freezing points by contact, for the internal temperature can be estimated by means of the chart without piercing. For instance, an undercooling point of −18° C. by contact makes the internal temperature −15.7° for the species of insect and the type of thermojunction used by the writer. The point thus determined coincides remarkably well with that obtained by different means—that is, by placing a number of insects in a

cabinet and lowering the temperature about 1° in 12 hours, and noting the point below which the insects can not go without freezing.

The thermocouple made for the combined readings may be used for these determinations also, the contact junction only being used. However, a couple with only the single contact junction will be found much more convenient. The essential features emphasized for combined readings, such as precooling of the junction holder, constancy of the cabinet temperature, and firmness of contact with the insect, apply, of course, to these determinations also. The freezing cabinet should be maintained at the temperature at which the correlation chart was made. Particular care should be taken to avoid injury to the specimens.

## SUMMARY

In low-temperature studies undercooling and freezing-point determinations provide valuable data. The piercing method of making the determinations produces shock to the organism and gives inaccurate readings of temperature. A means of making determinations by contact is described and detailed instructions for the construction of a contact thermocouple are given.

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